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Cougar Resource Selection in Two Mountain Ranges in Utah: A Study on Scale and Behavior

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COUGAR RESOURCE SELECTION IN TWO MOUNTAIN RANGES IN UTAH: A STUDY ON SCALE AND BEHAVIOR

by

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ABSTRACT

Cougar Resource Selection in Two Mountain Ranges in North-Central Utah:

A Study of Scale and Behavior

by

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Utah State University, 2010

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An understanding of habitat relationships is essential for managing hunted species, such as cougar, that are difficult to census. In the first phase of this study, I used aerial telemetry data to examine diurnal cougar resource selection at 2 scales, and compared results between 2 study sites, the Oquirrh Mountains and Monroe Mountain, Utah. In the second phase of this study, I used conditional logistic regression models and GPS collar data from the Oquirrh Mountains to determine whether cougar resource selection varied over 3 behaviors (prey caching, resting at a daybed site, and nocturnal activities) and 2 scales.

Results from phase 1 indicated that in general, during diurnal hours cougars selected for woodland cover types, moderate to steep (20-70%) slopes, canyon and steep hillside landforms, and home ranges with a higher density of edge. However, selection for these resources was not consistent at both study sites, scales, or for every cougar.

Small sample sizes and poor spatial accuracy of the aerial telemetry data likely precluded the ability to detect selection in every case.

Results from phase 2 indicated that cougar resource selection varied by behavior, and selection of some resources was detected only at certain scales. Cougar cache sites were characterized by southern and eastern aspects; lower elevation; avoidance of edge; a greater diversity of land cover types; canyon landforms (ridges were avoided); riparian, deciduous, and coniferous woodland; and deciduous and coniferous forest cover types. Cougars selected daybed sites that avoided western aspects and edges, were further from roads, closer to streams, higher in elevation, on moderate to steep slopes, and in rocky, deciduous woodland, and riparian cover types. During nocturnal activities, cougars avoided northern aspects, and selected areas that were closer to streams and roads, on edges and in canyon landforms, with gentler slopes, and rock, riparian, and deciduous woodland cover types. Results from cross-validation procedures confirmed that the models were reliable and predictive of cougar resource selection.

This study provides a comprehensive analysis of cougar resource selection over various scales and behaviors. Managers should use caution when using diurnal data to make conclusions about selection during other times of day or behaviors.

(286 pages)

Dedicated to T. and C., whom I lost before the end.

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LIST OF ACRONYMS AND ABBREVIATIONS

Acronym/Abbreviation	Definition
AGRC	Automated Geographic Reference Center
AIC	Akaike Information Criteria
AIC_c	Akaike Information Criteria corrected for small sample size
AML	Arc Macro Language
ATV	all-terrain vehicle
BLM	Bureau of Land Management
CA	compositional analysis
CDF	cumulative distribution function
CI	confidence interval
CMGWG	Cougar Management Guidelines Working Group
CMH	Cochran-Mantel-Haenszel
DCA	discrete choice analysis
DEM	digital elevation model
DLG	digital line graph
DOP	dilution of precision
F	female cougar
FDR	false discovery rate
FK	fixed kernel
GIS	geographic information system
GLM	generalized linear model
GPS	global positioning system
IIA	independence of irrelevant alternatives
K-S	Kolmogorov-Smirnov
LSCV	least squares cross-validation
M	male cougar
MCP	minimum convex polygon
MH	Mantel-Haenszel
OR	odds ratio
RSF	resource selection function
RSPF	resource selection probability function
SD	standard deviation
SWReGAP	Southwest Regional Gap Analysis Project
TPI	topographic position index
UDWR	Utah Division of Wildlife Resources
USGS	United States Geological Survey
UTM	Universal Transverse Mercator
VHF	very high frequency
VIF	variance inflation factor

INTRODUCTION

The cougar (*Puma concolor*) is the only large, obligate carnivore in North America that still persists in healthy numbers across broad areas without the need for intensive management beyond harvest limits (Lindzey et al. 1989, Logan and Sweanor 2001, CMGWG 2005). It therefore serves an important role as a top predator in maintaining the integrity of many western ecosystems (Noss 2001, CMGWG 2005). The cougar's resilience is evident in its adaptation to a wide range of environmental conditions, ability to navigate long distances across seemingly inhospitable terrain, high dispersal rate, and relatively quick recovery from population declines (Lindzey et al. 1992; Ross and Jalkotzy 1992, Beier 1993, Weaver et al. 1996, Logan and Sweanor 2001). Nevertheless, habitat loss and over-exploitation threaten the species in some parts of its range (Logan and Sweanor 2000).

Low density, vagile species like the cougar require both large areas and connectivity among populations to ensure persistence, and as a result they are sensitive to habitat loss and fragmentation (Beier 1993, Carroll et al. 1999, Sweanor et al. 2000, Crooks 2002). Cougar habitat is being diminished by rapid land use changes occurring in many areas of the West, including the Wasatch Front of Utah (Beier 1996, Murphy et al. 1999, Sunquist and Sunquist 2000, Logan and Sweanor 2000, McLaughlin 2003, Pierce and Bleich 2003). Urbanization, conversion of land to agriculture, and increases in rural residential development has reduced the quantity of cougar habitat as well as wintering range for ungulate prey. Dense urbanization also fragments cougar habitat by impeding

juvenile dispersal and expansion of highways increases cougar deaths by vehicle collisions (Mansfield 1986, Beier 1995, UDWR 1999, Logan and Sweanor 2001, Maehr and Cox 1995, Pearlstine et al. 1995, Pierce and Bleich 2003, CMGWG 2005). As human activity continues to expand into cougar habitat, cougar populations located around human housing or recreation areas may be further reduced by removal of individuals involved in encounters with people or that are responsible for pet depredations (Torres et al. 1996, UDWR 1999). Managers may also reduce cougar numbers in specific areas to control or prevent depredation of livestock, endangered species such as bighorn sheep (*Ovis canadensi*), or other prey populations. An understanding of cougar-habitat relationships will aid in managing conflict with prey species and humans as well as in identifying deteriorating habitat areas and potential dispersal corridors (UDWR 1999, Logan and Sweanor 2000).

Over-exploitation is perhaps the second greatest threat to cougars (Logan and Sweanor 2001). Because the species occurs in low densities and has a relatively low reproductive rate it can be susceptible to extinction, particularly where populations are small and isolated (Beier 1993, Logan and Sweanor 2001, Crooks 2002). This is evident in its endangered status in Florida, and extirpation from the eastern U.S. In addition, the cougar is elusive, wide-ranging, and solitary, making it difficult to survey and estimate accurate population numbers in order to manage harvest with precision (Ross et al. 1996, Logan and Sweanor 2000, Choate et al. 2006). Current cougar harvest levels in Utah are determined using habitat indices of prey and cougar densities, and the previous year's cougar harvest returns (UDWR 1999), a method which grossly overestimated cougar numbers in some areas of the state (Wolfe et al. 2004). Harvest return data does not

always reflect true population trends and populations may be declining before managers are aware (Logan and Sweanor 2001). The availability of high quality habitat provides a cushion against possible management errors stemming from uncertainties in setting harvest limits, particularly when combined with designated or de facto refugia (CMGWG 2005). For these reasons, cougar management requires a unified approach that incorporates both habitat and population management (Caughley 1994, CMGWG 2005).

Wide-ranging, highly mobile species like the cougar usually exhibit regional genetic and population processes and thus require assessment of habitat over large extents (Carroll et al. 1999, Anderson et al. 2004, CMGWG 2005). However, cougar range spans multiple continents and evaluating the relative importance of vegetative cover types and other resources over such a vast and diverse area is difficult and necessitates much generalization (Carroll et al. 1999, Pierce and Bleich 2003). The quality of cougar habitat varies considerably in terms of cover, prey abundance and availability, disturbance and land use changes, and vulnerability of cougars to hunting (Van Dyke et al. 1986b; CMGWG 2005). Generalized distribution maps lack consideration of the variability within blocks of habitat or the context of blocks within the surrounding matrix of unused areas (Maehr and Cox 1995, Wiens 1996, Sweanor et al. 2000, Turner et al. 2001). Long term research is needed on cougar habitat use patterns that integrate multiple scales and include a variety of environmental conditions in order to produce reliable maps of cougar density and habitat quality (CMGWG 2005).

In light of continuing increases in human populations, activity, and their potential impacts on cougars, an understanding of the habitat components that are important to the species is crucial to manage and plan for its conservation (CMGWG 2005). One goal of

cougar management in Utah is “to minimize loss of quality and quantity of existing critical and high priority cougar habitat” (UDWR 1999). However, it is necessary to first document and map habitat to provide a basis for monitoring any changes as well as to define and direct population and prey management (Hopkins et al. 1986, CMGWG 2005, McDermid et al. 2005). Further complicating the biological components of cougar management is the presence of a diverse, vocal, and often discordant group of stakeholders (UDWR 1999, Riley and Decker 2000, Teel et al. 2002). With the availability of more sophisticated telemetry equipment and statistical methods, habitat modeling is becoming an important tool in evaluating both sociopolitical and biological issues associated with cougar conservation (Laing and Lindzey 1991, CMGWG 2005).

RESEARCH OBJECTIVES

My primary research goal was to study cougar resource selection on the Oquirrh Mountains and on Monroe Mountain, Utah, over multiple scales and behaviors within a use-versus-availability framework. Animals make decisions at coarse temporal and spatial scales over a lifetime, as in home range selection, and at finer scales, such as over a few minutes and a few hundred meters (Rettie and McLoughlin 1999). To examine scale dependency, I took a 2-stage approach by first characterizing cougar resource selection at a relatively coarse scale using data collected via traditional diurnal telemetry methods. I then examined finer level decisions made by cougars using data acquired at the Oquirrh Mountain site via global positioning system (GPS) collars. Compared to the traditional telemetry data, the GPS collar data were more refined with respect to spatial accuracy, number and frequency of locations, temporal coverage (i.e., time of day), and the ability to extract behavioral information.

The objectives of the coarse level analysis were to quantify cougar diurnal selection of vegetation types, terrain features, and landscape, and to compare results from the 2 study sites. The coarse level analysis was conducted at 2 scales: home range selection versus availability of resources in the study area, and resource use versus availability within an individual cougar home range.

The objectives of the fine level analysis were to use GPS telemetry data from a set of cougars on the Oquirrh Mountains and discrete choice models to explain and predict cougar resource selection during 3 different behaviors (prey caching, resting at a

daybed, nocturnal movements) and at 2 different scales (within all of the home range versus within a small, localized area). Because the study of resource selection required delineation of home ranges as a sampling frame, I also examined cougar space use at various scales.

LITERATURE REVIEW

Cougar Habitat

Direct persecution and habitat loss due to deforestation, agricultural development, and human settlement led to the extinction of the cougar in eastern North America except in southern Florida (Young and Goldman 1946, Belden 1986, Johnson et al. 2001). In western North America, the species endured because of its solitary nature and ability to survive in rugged areas away from bounty hunters and human settlements (Young and Goldman 1946, Woodroffe 2001). Although its overall geographic range has been reduced by at least 50%, the cougar's current distribution remains one of the largest of the terrestrial mammals, spanning 100 degrees of latitude from British Columbia to Chile (Young and Goldman 1946, Nowak 1974, Logan and Sweanor 2000). Given this large range, cougar habitat varies widely but generally is a function of prey numbers and availability, and cover provided by vegetation and terrain (Seidensticker et al. 1973). However, variation in cougar density, distribution, habitat selection, and social structure relative to climate and vegetation communities, prey species composition, and prey densities are not well understood (Anderson 1983, Pierce et al. 2000b). Rarely seen even with tracking equipment, the cougar is one of the most difficult species to census (Seidensticker et al. 1973, Anderson 1983, Choate et al. 2006). The cougar's propensity and skill for hiding is an adaptation that is fundamental to understanding cougar habitat selection. Literature on cougar associations with prey, vegetation, and topography as well as cougar response to disturbance and landscape patterns is reviewed below. Cougar temporal activity patterns and behaviors are also discussed.

Prey

Cougars are flexible in their feeding ecology and feed on a wide variety of prey species, from large ungulates to small mammals and birds, depending on the abundance and types of prey that are available (Anderson 1983, Iriarte et al. 1990, Sunquist and Sunquist 2000). In North America, the cougar primarily preys on deer (*Odocoileus hemionus, O. virginianus*), which usually accounts for about 60-90% of its diet; it also preys on elk (*Cervus elaphus*), moose (*Alces alces*), feral horses (*Equus caballus*), porcupines (*Erithizon dorsatum*), bighorn sheep (*Ovis canadensis*), domestic livestock (primarily sheep but also cattle), and a variety of smaller mammals (Robinette et al. 1959, Ackerman et al. 1984, Iriarte et al. 1990, Turner et al. 1992, Sweitzer et al. 1997). It is unlikely that cougar populations could be sustained in North America in the absence of large ungulates (Ackerman et al. 1986, CMGWG 2005). However, small mammals may be an important component of cougar diet for some populations, especially in summer and in more arid regions (Seidensticker et al. 1973, Ackerman et al. 1984, Leopold and Krausman 1986, Cunningham et al. 1999, Rosas-Rosas et al. 2003). In Central and South America, the species survives on the abundance and variety of small to medium size prey, with ungulates making up only 35% of the cougar's diet (Young and Goldman 1946, Iriarte et al. 1990, Branch et al. 1996, Taber et al. 1997, Franklin et al. 1999). Competition with sympatric large carnivores may impact cougar prey selection but this has not been well studied (Koehler and Hornocker 1991, Husseman et al. 2003).

Cougar distribution in western North America is closely associated with ungulate movement patterns and habitat at broad scales (Robinette 1959, Anderson 1983). In regions with heavy snow, cougars usually follow migrating deer by shifting their winter

activity to lower elevations where deer congregate, or by occupying 2 disjunct seasonal home ranges (Seidensticker et al. 1973, Logan and Irwin 1985, Laing 1988, Pierce et al. 1999, Katnik 2002). However, not all cougar populations appear to track deer movement or changes in densities. During a severe winter in Arizona when deer concentrated in lower elevations some cougars starved to death rather than move with the deer even though the habitat appeared suitable for cougars (Shaw 1980, Van Dyke et al. 1986b).

Although the distributions of deer and cougar are similar they are not identical. Clearly sufficient prey numbers are required for cougar occupancy, but not all prey in a general area may be accessible to cougars if terrain and vegetative cover are deficient (Seidensticker et al. 1973, Sunquist and Sunquist 2000). Most felids are found in forested environments and, except for the cheetah (*Acinonyx jubatus*), all have morphology adapted for short, quick ambush of prey rather than long distance pursuits. They require camouflage and cover to approach prey at close range without being detected, and are known to abandon the hunt if sighted by prey (Anderson 1983, Eisenburg 1986, Kruuk 1986, Branch 1995). Pronghorn antelope (*Antilocapra americana*), which primarily occur in open plains, are not usually a component of cougar diet and are only killed when they enter areas where vegetation or terrain provide cover (Ockenfels 1994, Logan and Sweanor 2001). Similarly, ungulates in Yellowstone National Park are common in grasslands and agriculture but cougars rarely make kills in these areas (Murphy 1998). While deer are found in areas that cougars do not use, cougars are also known to use areas that deer do not habitually use (Hansen 1992). For example, winter kill sites in the Sierra Nevada were clumped in lower elevations within cougar home ranges, suggesting

cougars used particular areas for hunting compared to overall home range use (Pierce et al. 2000b).

Because cougar distribution can not be fully explained by the distribution of prey, other factors influencing predator success may be important (Pierce et al. 2000b, Husseman et al. 2003). Jalkotzy et al. (1999) found that variation in prey numbers was not a significant predictor of cougar use but indices of prey vulnerability based on stalking cover were important predictors. Stalk-and-ambush predators like the cougar may be more limited by the availability of habitat that provides stalking cover than by prey densities in some areas (Kruuk 1986, Hopcraft et al. 2005). That is, both the abundance and the accessibility of prey are important factors in cougar habitat selection (Seidensticker et al. 1973).

Vegetation

A testament to its adaptability, the cougar occurs in a wide variety of biomes across its range, including semi-desert to mesic woodlands and shrublands, chaparral, desert and forested mountains, and forested swamps. However, there are no reproducing populations in desert flats, open grasslands, or agricultural areas (Findley et al. 1975, CMGWG 2005). Although the cougar is a habitat generalist some environments are consistently used to a higher degree than others, indicating conditions that likely enhance the success of raising kittens and catching prey (Rosenzweig 1981, Orians and Wittenberger 1991, Hall et al. 1997). In western North America, cougars use areas with diverse topography and vegetation, which provide an advantage in terms of the amount and variety of cover available. In addition to being used for stalking prey, cover also

provides security for resting during daylight hours, feeding on cached prey, and protection of kittens (Seidensticker et al. 1973). Beier et al. (1995) documented cougars being mobbed by crows (*Corvus* sp.) at prey carcasses.

Seidensticker et al. (1973) first reported that 95% of cougar radio-locations and tracks were in "timbered and/or rocky, broken, terrain" in their study site in Idaho, and other cougar studies in mountainous areas have related similar findings. In mesic mountain ranges, cougars use aspen (*Populus tremuloides*) forests, mixed aspen-conifer forests, and mixed coniferous forests more frequently than expected as compared to their availability. Mixed coniferous forests with a diversity of species such as ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), Douglas fir (*Pseudotsuga menziesii*), and juniper (*Juniperus* spp.), are used more frequently than coniferous monocultures (Logan and Irwin 1985, Koehler and Hornocker 1991, Laing and Lindzey 1991, Williams et al. 1995, Katnik 2002). Cougars use higher elevation forests composed of spruce-fir (*Picea -Abies*) more frequently in summer and fall months (Koehler and Hornocker 1991, Laing and Lindzey 1991). Conversely, during winter months in northwestern Utah and southwestern Idaho, cougars made more kills in pinyon (*Pinus spp*)-juniper than in spruce-fir (Laundre and Hernandez 2003). Where forests are rare or absent, cougars are found in chaparral (Dickson and Beier 2002) and pinyon-juniper woodlands (Campbell 1998). At the finer scales cougars frequent areas with vegetation types that are important to deer, such as bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus ledifolius*), and Gambel oak (*Quercus gambelii*) (Logan and Irwin 1985, Laing 1988, Jalktozy et al. 1999).

Vegetative structure in terms of understory cover, overstory cover, and height are important predictors of habitat used by cougars (Logan and Irwin 1985, Laing 1988, Branch 1995, Husseman et al. 2003, Laundre and Hernandez 2003). Cougars used open stands of ponderosa pine or pinyon-juniper (i.e., mostly sagebrush, few trees) less frequently in southern Utah than stands with an oak brush understory (Laing and Lindzey 1991). In timbered regions, cougars frequent forests with greater amounts of understory cover (Williams et al. 1995, Jalktozy et al.1999). Moderately dense cover is probably ideal for stalking so that the cougar can remain unseen but still move about and sight prey (Lindzey 1987). Cougars used areas with greater canopy cover in arid southern Utah (Laing and Lindzey 1991) but did not use canopy cover selectively in mesic, forested mountains of Washington (Katnik 2002). In addition to providing stalking cover and security during diurnal hours, canopy cover also probably aids in thermoregulation during various times of day, seasons, and behaviors.

Cougars likely respond to vegetation structure when selecting natal den sites. Natal dens are simply inaccessible areas selected by the mother for parturition, and are not necessarily associated with a cave, nor are sites enlarged or modified by the mother (Beier et al. 1995, Maehr et al. 1989). They may be found in thick, impenetrable brush, boulder piles or rocky cliffs and overhangs (Maehr et al. 1989, Beier et al. 1995, Bleich et al. 1996, Logan and Sweanor 2001, Benson et al. 2008). Thermoregulation as a function of canopy cover appears to be important in the selection of natal den sites in climates with hot summers (Bleich et al. 1996, Jalkotzy et al. 1999).

Results from various studies have been conflicting in terms of determining the relative frequency with which cougars may use areas that lack cover or if there is some

maximum sized open area they will not cross, either in daily movements or during dispersal (Comiskey et al. 2002, Maehr et al. 2004). All studies to date have found that during diurnal hours, cougars avoid open vegetation systems lacking some form of cover. Desert shrublands and sagebrush (*Artemisia* spp.) shrublands are usually avoided, but grasslands, open wetlands, agriculture, and urbanized areas are even more rarely used (Logan and Irwin 1985, Belden et al. 1988, Laing and Lindzey 1991, Dickson and Beier 2002, Katnik 2002). Tracking data often indicate that cougars move using patches of cover, skirting open areas (Williams et al. 1995, Jalktozy et al. 1999). However, Seidensticker et al. (1973) noted cougar tracks also crossed open hillsides. Given Beier et al.'s (1995) description of cougar movement and travel bouts, use of open areas may vary depending on whether the cougar is stalking prey or decisively traveling to get to a particular place. Cougars will travel faster through some habitat types than others (Dickson et al. 2005). Openness is not an absolute barrier because cougars will travel across desert valley bottoms when dispersing between arid mountain ranges (Sweanor et al. 2000).

While pursuit likely begins in or near vegetative cover, it is not clear if prey is captured more easily in open areas or in cover (Pierce and Bleich 2003). Hornocker (1970) reported cougars in the forests of central Idaho had a success rate of approximately 80% when killing mule deer, but this rate was substantially lower (10%) when cougars killed small prey in open shrub systems (Branch 1995). Results from studies that used snow tracking of kill sites have suggested a greater number of kills occur in areas with vegetative cover and rugged terrain such as forests, bluffs or brushy ravines (Hornocker 1970, Williams et al. 1995, Jalkotzy et al. 1999). When kills

occurred in open habitat types in the Bighorn Mountains of Wyoming, they were always within 250 m of concealing vegetation (Logan and Irwin 1985). Bishop et al. (2005) found mule deer fawns were killed by cougars in areas with greater cover, structure, and slope compared to fawns that died of other causes. However, other studies report that kills are made more frequently in open areas. Husseman et al. (2003) found kills more frequently in open, low elevation shrublands than in dense coniferous forests. Pierce et al. (2004) concluded that cover did not enhance the likelihood of a cougar making a kill in the Sierra Nevada because kills were made more frequently in open vegetation than in heavy cover where deer preferred to forage. Porcupines also appear to be killed more frequently by cougars in open grass or shrublands compared to wooded areas (Sweitzer 1996), though smaller prey may be difficult to see in wooded brush. These conflicting results may be a function of not considering the distance of the kill from the edge of cover, using different definitions of cover (e.g., understory vs. overstory), or different scales (e.g., microsite vs. coarse habitat types) (Husseman et al. 2003, Laundre and Hernandez 2003). Variation in the location of kill sites may also relate to differences in the particular environment and types of prey available.

Some studies indicate environments with a high rock component are used to a greater degree than expected by cougars. For example, Logan and Irwin (1985) found cougars in the Bighorn Mountains of Wyoming frequently used mountain mahogany woodlands, a system that is adapted to rocky ridges, cliffs, and rimrock (Comer et al. 2003). Within extensive monocultures of pinyon pine (*Pinus edulis*) and juniper woodlands, cougars preferred areas which contained many boulders, and also frequently used lava rock and sandstone ledges (Laing 1988). However, Campbell (1998) reported

avoidance of rock at a meso-scale. Open expanses of bare rock without vegetative cover are avoided (Laing and Lindzey 1991, Williams et al. 1995). The use of rocky areas may be more important at a microsite level that is not captured in land cover maps typically used in habitat studies.

Quantitative studies conducted in more arid climates report that cougars often use riparian zones, possibly because prey congregate in these areas (Laing and Lindzey 1991, Beier 1995, Dickson and Beier 2002, Dickson et al. 2005). However, in mesic forests cougars have not been found to use riparian areas selectively (Logan and Irwin 1985, Williams et al. 1995, Husseman et al. 2003). In the Sierra Nevada, cougars were documented using riparian areas for natal den sites (Bleich et al. 1996). However, Florida panthers avoided wet lowland habitat types (e.g., wet forests or swamps) in favor of drier upland types when selecting natal den sites (Benson et al. 2008). Cougars are apparently not limited by access to water (Young and Goldman 1946).

Topography

In the mountainous West, cougars are usually found at middle to upper elevations, and generally do not use the highest elevation alpine zones or valley basins (Ashman et al. 1983, Laing and Lindzey 1991, Williams et al. 1995, Germaine et al. 2000, Sweanor et al. 2000, Laundre and Hernandez 2003, Pierce et al. 2004). Cougars seem to prefer rugged, steep topography and avoid gentle slopes (Logan and Irwin 1985). Kill sites are often associated with greater terrain complexity and steep slopes (Hornocker 1970, Jalkotzy et al. 1999). Steep slopes may promote stalking from above, which potentially increases attack speed (Jalktozy et al. 1999). In some cases, a diversity of terrain may

also enhance the ability to sight prey by providing views of a greater area (Hopcraft et al. 2005).

Many studies report that cougars frequently use canyons and draws as well as ridge tops for travel, for scent marking, and as cover for approaching prey (Seidensticker et al. 1973, Logan and Irwin 1985, Laing 1988, Ruth 1991, Williams et al. 1995, Logan and Sweanor 2001). Dickson and Beier (2006) found that cougars traveled more frequently across canyon bottoms and gentle slopes than ridges and steep slopes when moving through southern California chaparral. In navigating through urbanized areas in this region, cougars were more likely to use freeway underpasses that were aligned with drainages (Beier and Loe 1992). Movement paths generally meander, crisscrossing ravine bottoms and patches of cover (Seidensticker et al. 1973, Hopkins et al.1986, Beier 1995, Dickson et al. 2005). These types of movements likely maximize the chances of encountering prey, and also put the cougar in an optimal position to attack (Sunquist and Sunquist 2000). Cougars tend to move parallel to topographic contours rather than up steep slopes when traveling, which probably reduces energetic costs (Seidensticker et al. 1973, Dickson et al. 2005).

Terrain ruggedness appears important in influencing cougar locations and movements at fine scales, but it is also predictive of overall cougar distribution at larger, state-wide scales (Riley and Malecki 2001). However, use of rugged areas in the West may be an artifact of selection for the vegetative cover that occurs in these areas. That is, forests and woodlands with the cover that cougars require occur in more rugged terrain whereas open shrublands, grasslands, and agricultural areas occur in flat valley bottoms.

Furthermore, the species lives in the flat terrain of Florida but dense vegetation in the swamps and forests apparently provides abundant hiding cover.

Aspect was important in the mountains of Nevada, where in winter cougars were found more often on south-facing slopes with shallow snow and plentiful deer (Ashman et al. 1983). In the milder climate of southern California, cougars did not select for any particular aspect (Dickson and Beier 2002).

Landscape Patterns

Spatial heterogeneity is an important element of habitat selection, and including measures of landscape pattern may improve habitat models (Porter and Church 1987, Mysterud and Ims 1998, Lawler and Edwards 2002). Many animals select for a mosaic of habitat types, each of which has different costs and benefits in terms of reproduction and survival (Rettie and McLoughlin 1999, Cox et al. 2006). In addition, the juxtaposition of types, patch density, size, and arrangement, and amount of edge may be of equal or greater importance in influencing selection than the quantity of available habitat types alone. Previous studies have concluded that landscape pattern influences habitat selection by felids, including the Florida panther (Maehr and Cox 1995), bobcat (*Lynx rufus*) (Nielsen and Woolf 2002), Iberian lynx (*Lynx pardinus*) (Fernandez et al. 2003, and ocelot (*Leopardus pardalis)* (Jackson et al. 2005).

The configuration of patches of cover and edge may be an important component of cougar habitat selection in terms of optimizing hunting conditions. Cougars respond to a localized scale when stalking prey by confining hunting to specific habitat patches (Husseman et al. 2003, Laundre and Hernandez 2003). In particular, cougars frequently

use edges and ecotones (Belden et al. 1988, Laing 1988, Williams et al. 1995, Holmes and Laundre 2006), which provide cover for approaching prey at close range and allow the cougar to sight prey in adjacent open patches. Snow-tracking data have indicated that cougars use cover to get as close as possible to prey before attacking (Logan and Irwin 1985). Rare live observations of cougar kills have documented that an attack is launched once the prey is within 2 -10 m (Beier et al. 1995, Branch 1995). Usually the chase is short once pursuit begins; reported chase distances ranged from 25 – 90 m (Beier et al. 1995, Jalkotzy et al. 1999, Laundre and Hernandez 2003). One study found that 72% of kills were made in edge areas compared to open patches or within forests (Laundre and Hernandez 2003).

A study on the Florida panther asserted that the cats would not use forest patches smaller than 500 ha (Maehr and Cox 1995) but these results have been disputed by others (Comiskey et al. 2002, Beier et al. 2003). Katnik (2002) reported that cougars selected home ranges with a greater number of small openings. Benson et al. (2008) reported that Florida panther den sites were neither positively nor negatively associated with edge or patch size. However, their study was at the macroscale using coarse landcover GIS data, and it is likely that panthers and cougars respond to microsite characteristics when selecting a home range. There has been little work completed on other aspects of spatial heterogeneity and cougar habitat selection.

Disturbance

Cougars tolerate moderate levels of disturbance depending on the size of the disturbed area, its permanency, and frequency (Van Dyke et al. 1986b). They may be

attracted to burned areas depending on how recently the fire occurred and the length of time before regrowth occurs (Belden 1986, Dees et al. 2001). Cougars also are known to use burned areas if rock or cliffs are present for cover (Williams et al. 1995). However, they apparently avoid large, open burns (as large as 1.6 km across; Seidensticker et al. 1973) and large-scale logging areas (Van Dyke et al. 1986b). One study documented a cougar death caused by asphyxiation after a large fire encompassed her home range (Fescke 2003). Cougars also may shift the timing of activity to avoid disturbance from logging activities (Van Dyke et al. 1986b).

Where cougars live near human development, land use practices and other human influences impact their habitat, though apparently they can habituate to the noise of highways, air-traffic, and rock quarries (Belden 1986, Jalkotzy et al. 1999, CMGWG 2005). In southern California, cougars moved through low density housing but a density of more than 20 dwellings per hectare apparently was insurmountable (Beier 1995). In mountainous areas of the West, housing and paved roads usually occur at lower elevation areas not suitable for cougars to establish home ranges (Van Dyke et al.1986b). However, populations are impacted by valley development because it impedes the dispersal of juvenile cougars to other mountain ranges. Cougars will cross highways and travel under bridges, usually where cover exists on either side (Belden 1986, Beier 1995, Ruth et al. 1998, Gloyne and Clevenger 2001). Vehicle collisions are a major source of mortality for cougars living in highly fragmented habitat (Maehr et al. 1991, Beier 1995). Even in relatively pristine regions, expansions of roads and the resulting increases in traffic volume can increase cougar road-kills (Sweanor et al. 2000).

Cougars avoid major highways when selecting a home range (Dickson and Beier 2002), but they generally tolerate dirt roads and trails that commonly occur throughout less human dominated cougar habitat in the West (Van Dyke et al. 1986a, Laing 1988, Jalktozy et al. 1999, Fecske et al. 2003). Unpaved roads and trails may even facilitate movement through thick vegetation (Beier 1995, Dickson et al. 2005). However, they seem to cross improved dirt roads less frequently than unimproved roads (Fecske et al. 2003). Cougars will cache prey and use daybed sites near heavily used trails and campgrounds (Beier 1995, Ruth 1991, Jalkotzy et al. 1999, Sweanor et al. 2008). However, Jalkotzy et al. (1999) found that in both summer and winter, cougars avoided heavily used roads and trails where cougar hunting and other human activity was concentrated, but they did not avoid roads and trails with low human use. Roads increase hunter access, which combined with the increase in the use of four-wheelers and snowmobiles, allow more efficient hunting and may leave fewer refuges for cougars (Hemker et al. 1984, Logan and Sweanor 2001).

Temporal Activity Patterns

For the majority of a 24-hour period cougars are inactive and only travel about 25% of the time on average (Ackerman et al. 1986, Beier et al.1995). During daylight hours particularly, the cougar rarely moves more than a few hundred meters (Hopkins 1989, Beier et al. 1995). Unless the cougar has cached prey, it will actively hunt during the crepuscular and nocturnal hours (Van Dyke et al. 1986b, Anderson et al. 2003) in short bouts of travel alternating with periods of rest (Beier et al. 1995). Once a large prey item has been killed, the carcass is cached and fed on over multiple nights (range of 1-8

nights reported) with the cougar moving from a daybed to the cache site to feed during nocturnal hours (Beier et al. 1995, Anderson and Lindzey 2003). Daybed sites are usually within a few hundred meters of the carcass, but may be as far as 4.2 km away (Beier et al. 1995, Laundre and Hernandez 2003). Cougars use cover for caching prey after making a kill, and may abandon a carcass if it cannot be moved to a secure area (Logan and Irwin 1985). They are reported to drag the carcass as far as 350 m from the kill site to where it is cached, though usually it is cached within 0 to 80 m (Beier et al. 1995, Laundre and Hernandez 2003). The killing of large prey is a considerable energy investment and hiding remains in dense cover probably prevents decomposition and loss of biomass to conspecifics or other species (Seidensticker et al. 1973, Beier et al. 1995, Sunquist and Sunquist 2000, Laundre and Hernandez 2003).

The timing of cougar activity can vary depending on season, climate, or the presence of kittens. Seidensticker et al. (1973) reported that in Idaho, cougars were more active during the day in the summer compared to winter, which was likely related to the wider distribution of mule deer and the availability of diurnal ground squirrels as prey during this season. Ackerman et al. (1984) also reported cougars captured both diurnal and nocturnal prey species. The Florida panther was active during the day and night in winter but rarely moved during the day in summer (Belden 1986). Seasonal effects most likely relate to the timing of prey movements and temperature.

Females with kittens show different temporal activity patterns than other cougars. Females with newborn kittens restrict activity to a localized area around the natal den (Seidensticker et al. 1973, Hemker et al. 1984). Denning females also return to cache sites earlier in the nocturnal period than other adults, possibly to avoid conspecific

interaction (Pierce et al. 1998). These behaviors likely reduce the chances of kitten deaths from other predators and infanticide by male cougars (Maehr et al. 1989, Beier et al. 1995, Bleich et al. 1996, Logan and Sweanor 2001).

Because cougars are primarily active during crepuscular and nocturnal hours (Beier et al. 1995, Franklin et al. 1999, Pierce and Bleich 2003), conclusions about habitat preference may be erroneous or incomplete when based solely on diurnal telemetry, presumably collected when cougars are resting at daybed sites (Beyer and Haufler 1994, Kernohan et al. 2001). Elk and other large carnivores, such as bears (*Ursus arctos, U. americanus*), select different nocturnal habitat compared to diurnal habitat (Beyer and Haufler 1994, Belant and Follmann 2002). Most cougar studies to date have used only diurnal data, and have concluded unequivocally that cougars use areas of greater vegetative or topographic cover compared to their relative availability during diurnal hours (Logan and Irwin 1985, Laing and Lindzey 1991, Williams et al. 1995, Dickson and Beier 2002, Beier et al. 2003). Laing (1988) compared nocturnal ground telemetry and tracks with diurnal aerial telemetry and concluded that diurnal and nocturnal habitat use was similar. However, other studies that used nocturnal data indicated that cougars may use a broader range of habitat types during nocturnal hours compared to diurnal hours (Franklin et al. 1999, Pierce et al. 2000a, Dickson et al. 2005). Pierce and Bleich (2003) suggested that these disparate results may be due to variation in habitat conditions.

Cougars may use different habitat for different activities (e.g., hunting vs. resting). Pooling data across all activities could be problematic because resources used for the dominant behavior appear more frequently in the pooled dataset and resources

associated with rare behavior appear less frequently, and overall selection will be for the resource used in the most common activity (Cooper and Millspaugh 2001). If a particular resource is the least chosen resource overall because it is common on the landscape but it is always chosen for a rare activity, pooled data will predict avoidance of that resource.

Statistical Methods for Studying Resource Selection

The choice of an analytical method for studying resource selection is a "complex and sometimes controversial" decision, as evident by the large body of literature on resource selection methods (Alldrege and Griswold 2006). There is no one method that is best at controlling both Type I and Type II errors (Alldrege and Ratti 1986, 1992). The decision should be based on the research objectives, study design, data availability, and ability to meet the assumptions of the specific test (Alldrege and Ratti 1992, Manly et al. 2002). Older methods have previously been reviewed by White and Garrott (1990) and Alldredge and Ratti (1986, 1992). More modern methods have been reviewed by Erickson et al. (2001), Manly et al. (2002), Keating and Cherry (2004), McDonald et al. (2005), Alldredge and Griswold (2006), and Thomas and Taylor (2006). Methods specifically applicable to this study are reviewed below.

Resource selection studies that collect radio-telemetry data most commonly compare an animal's use of resources to availability because resource use may change if the availability of that resource changes in a given area (Manly et al. 2002). Selection is said to occur when use is disproportionate to availability (Johnson 1980). Factors influencing selection may vary by scale; therefore, a hierarchical approach to resource selection is often used (McDonald et al. 2005). Johnson (1980) defined 4 hierarchical

orders of selection: first order, or a species geographic range; second order, or selection of a home range within a study area; third order, or selection of locations within a home range; and fourth order, or selection of a specific area within a habitat patch (microsite selection). There are 2 basic approaches to studying resource selection. Sampling-design-based methods characterize the habitat types (or other resources) by examining the amount of use, and hypotheses are tested based on random sampling variation. In contrast, model-based methods characterize the locations, examining which variables contribute to selection by comparing used to unused (or a sample of available) locations (Garshelis 2000, Manly et al. 2002, Alldredge and Griswold 2006).

Sampling-Design-based Methods

Two of the most common design-based methods for studying resource selection with categorical data are compositional analysis and the chi-squared goodness-of-fit test. Compositional analysis (CA) is an application of multivariate analysis of variance (Aebischer et al. 1993). In CA, resource use for each animal is defined as a vector of the proportions of habitat types from all radiolocations (third-order selection) or within the home range (second-order selection). Availability is defined as a vector of the proportion of vegetation types in each home range (third order) or within the study area (second order). Resource selection is probably best analyzed with multivariate techniques given that the use of one resource type generally rules out use of another type at the same time, and CA is well-designed in this respect (Aebischer et al. 1993, Manly et al. 2002, Alldredge and Griswold 2006). In addition, CA removes the unit-sum constraint by a log-ratio transformation of the proportions (Aebischer et al. 1993). The

unit-sum constraint occurs because the proportions of used and available resources must sum to 1 with compositional data. This results in a lack of independence because a change in the proportion of one vegetation type changes the proportions of the other types (Aebischer et al. 1993). This method does not require radiolocations to be independent since the animals are the experimental unit. However, it does require independence among animals because inferences are made about the general population (Otis and White 1999, Alldredge and Griswold 2006). This assumption may be difficult to meet for species that are territorial or that may otherwise be influenced by other individuals when selecting a home range, such as with cougar.

While CA has some advantages and is often promoted as the "preferred" method for studying resource selection with categorical variables (Beier et al. 2003, Bingham and Brennan 2004), the log ratios can be difficult to interpret, multivariate normality is required, and the compositions must be equally precise (i.e., equal number of radiolocations) (Thomas and Taylor 2006, Erickson et al. 2001, Dasgupta and Alldrege 2002). CA also requires that all animals select habitat in a similar way (Thomas and Taylor 2006), an assumption rejected by Alldredge et al. (1998). Furthermore, this method requires that all habitat types be both available to and used by all animals because the log ratio transformation cannot be calculated on zeroes (Aebischer et al. 1993). To analyze data from animals that show 0% use of a particular habitat type, Aebischer et al. (1993) suggested lumping types together, excluding the type if it is rare, or substituting a small positive value for the zero. However, it has been demonstrated that Type I errors increase when zeroes are replaced with small values (Bingham and Brennan 2004). For animals that do not have all habitat types available for use, Aebischer et al. (1993)

suggested either dropping the animal or attempting one of several other complex solutions (Dasgupta and Alldredge 2002). In addition to the challenges in handling zeroes, several studies have demonstrated that CA may be more generally prone to high Type I error rates (Pendleton et al. 1998, Dasgupta and Alldredge 2002, Bingham and Brenann 2004) or may produce results that are not consistent with known habitat requirements (McClean et al. 1998). Literature from other fields of research also describe problems implementing CA in practice (geology: Bohling et al. 1998, Rehder and Zier 2001; archaeological science: Tangri and Wright 1993, Baxter and Freestone 2006).

Distance-based measures of resource use rather than proportions have also been proposed for CA (Conner et al. 2003). However, this does not solve the problems with zeroes, and one study found questionable results using this method (Dussault et al. 2005). As an alternative to CA for studying second-order resource selection, Katnik and Wielgus (2005) suggested the use of cumulative distribution functions (CDF) to compare proportions of resource types in animal home ranges to proportions from simulations of random home ranges. Vegetation types are not uniformly distributed and are unlikely to occur in the same proportions in a home range as they do in an overall single measure of a larger study area (Porter and Church 1987, Wilson et al. 1998). Random home range simulations reduce Type I errors by making estimates of availability spatially-explicit (Katnik and Wielgus 2005). This method uses the number of animals as the sampling unit and makes conclusions at the population level.

Chi-squared tests are a classic approach to testing hypotheses about resource selection, and are easy to use and interpret (Alldredge and Griswold 2006). The chi-

squared test for goodness-of-fit tests the null hypothesis that observed use occurs in proportion to availability, where expected counts are calculated from the proportions of available habitat types (White and Garrott 1990). The test determines whether selection is occurring and is followed by estimation of confidence intervals around each habitat type to identify which types are selected or avoided (McDonald et al. 2005). Chi-squared tests are usually applied to third-order selection, or other designs (see Manly et al. 2002) that quantify individual use via counts of radiolocations.

The chi-squared methods may make inferences towards the population of animals or to the individual animal level, depending on assumptions of independence among animals and among radiolocations, respectively (Manly et al. 2002, Alldredge and Griswold 2006). The chi-squared test is often erroneously applied by confusing appropriateness of tests of homogeneity versus goodness-of-fit (Jelinksi 1991), or by pooling data collected on individual animals and running a single test before determining if individuals are selecting habitat in the same way (White and Garrott 1990, Alldredge and Griswold 2006). Unless individuals are not marked or there are few locations per animal (e.g., Neu et al. 1974), chi-squared tests should be run on individuals (White and Garrott 1990). When individuals can be considered independent, the individual chi-square statistics may then be summed for an overall population-level test for habitat selection (White and Garrott 1990, Manly et al. 2002).

Individual-based approaches to quantifying resource selection have advantages, including allowing comparison of the variation among individuals, properly weighting individuals based on their number of radiolocations, identifying individuals that may use resources differently from the others, and ability to identify potential differences in

subgroups (age, gender) (White and Garrott 1990, Alldredge and Ratti 1992, Manly et al. 2002). Examining individual selection may be the only viable approach if the species under study is territorial (Manly et al. 2002). White and Garrott (1990) and Manly et al. (2002) suggested that analysis could proceed in stages with the individual used as first stage units and the population used as second stage. If radiolocation data are pooled over animals then inference is limited to the marked set of animals, which are considered a fixed effect (Erickson et al. 2001). If the animals are the sampling unit (rather than the radiolocations) and they are randomly selected then inferences may be made to the larger population of animals (Erickson et al. 2001).

Simulation studies have demonstrated that chi-squared tests using both the pooled method (Neu et al. 1974) and individual-based method (White and Garrott 1990) consistently control Type I errors, and perhaps are somewhat conservative (Alldredge and Ratti 1986, Leban et al. 2001, Dasgupta and Alldredge 2002, Bingham and Brennan 2004). McClean et al. (1998) also found that results from the Neu method were consistent with known habitat requirements. However, the Neu method had high Type II errors, especially when the number of habitat types was small (Alldredge and Ratti 1986). One of the primary criticisms of chi-squared methods is that they do not deal with the unit-sum constraint, which imposes a correlation in the cells of the contingency table (Dasgupta and Alldredge 2002). However, this criticism does not necessarily invalidate the conclusions of the test (McClean et al.1998, Alldredge and Griswold 2006). Another disadvantage of the chi-squared method is that it does not address the multivariate nature of resource selection (Manly et al. 2002).

Selection ratios are another approach to studying selection for a single categorical resource variable. Rather than testing for overall selection, a selection ratio gives the relative probability of use for a particular habitat type (or other categorical variable), assuming all resource units are available and accessible (Manly et al. 2002). Relative measures of habitat use are probably more suitable to resource selection studies because habitat changes over a species range (Arthur et al. 1996). The ratio is calculated by dividing the proportion used by the proportion available. A ratio > 1 indicates selection for a habitat type, a ratio < 1 indicates selection against a habitat type, and a ratio of 1 indicates no selection (Manly et al. 2002). The ratio does not fluctuate with inclusion or exclusion of habitat types that are rarely used (Manly et al. 2002). When examining more than one independent variable the selection ratios can be generalized to the resource selection function (RSF), which estimates the relative probability that a particular resource unit is selected (Manly et al. 2002). One argument for using selection ratios is that under weighted distribution theory, the ratios (and the RSFs) are weighting functions, which transform the available distribution into the used (Johnson et al. 2006, Thomas and Taylor 2006). Data that are relative rather than absolute, such as use-availability data, may be best characterized using ratios (Aitchison 1986).

Model-based Methods

While hypothesis testing methods remain an important and commonly used statistical approach, resource selection studies have recently moved from these deductive approaches to empirically-based, inductive modeling, such as generalized linear models (GLM) (Erickson et al. 2001, Alldredge and Griswold 2006). This is consistent with the

general trend in ecological studies towards more quantitative and predictive techniques (Turchin 1998). Because null versus alternative hypothesis testing generates less informative results than considering multiple hypotheses (Anderson et al. 2000), and because resource selection studies are usually observational rather than manipulative, data on resource selection may be best analyzed with exploratory, modeling-based approaches (Garton et al. 2001). Because statistical models are designed to be multivariate they can identify the relative importance of different environmental variables (Garton et al. 2001). That is, models describe the nature of an association rather than simply determining whether an association exists (Stokes et al. 2000). Modeling approaches have the added capability of being spatially explicit by mapping the predicted probability of resource use (Erickson et al. 2001, Garton et al. 2001, Manly 2002, Nielsen et al. 2005).

Methods used to model animal resource selection are similar to those used to model species distributions with presence-absence data, except that the interest is in estimating probability of use rather than probability of presence, and individual animals are usually marked and monitored (Pearce and Boyce 2006). Binary logistic regression is the most commonly applied statistical model in resource selection studies (Thomas and Taylor 2006); however, there has recently been some debate over its application (Keating and Cherry 2004, Johnson et al. 2006, Pearce and Boyce 2006). Proper interpretation of logistic models requires a clear understanding of study design and assumptions (Keating and Cherry 2004, Johnson et al. 2006, Pearce and Boyce 2006). Using logistic regression to predict probability of use requires random sampling where the researcher first selects random locations and then determines if each location is used or unused (Keating and

Cherry 2004). However, in a use-availability design resource use is measured at known animal locations and availability is measured at a sample of randomly placed locations within a home range or within a study area (Erickson et al. 2001, McDonald et al. 2005). Because this design does not identify unused areas, the random sample of available locations could be contaminated with an unknown proportion of use locations along with unused locations (Garshelis 2000, Keating and Cherry 2004). There is some question as to the impact of contaminated samples. Some authors have indicated that the contamination rate must be substantial (> 20%) to invalidate relative probability estimates (Nielson et al. 2005, Johnson et al. 2006). Contamination also reduces the power to detect selection since use data and availability data are not mutually exclusive (Buskirk and Millspaugh 2004).

Another problem with applying logistic regression to use-availability studies is that when separate samples are taken of use and availability the sampling proportions of these 2 distributions are not known (Pearce and Boyce 2006, Thomas and Taylor 2006). The likelihood of a particular location being used is dependent on both the probability a location was selected in each sample and the probability distribution of the covariates (Hosmer and Lemeshow 2002). In use-availability designs, the probability of use cannot be estimated directly (i.e., the resource selection probability function, or RSPF), but rather indirectly through estimates of relative probability (the RSF) (Manly et al. 2002, Pearce and Boyce 2006). Relative probability of use gives the likelihood of a resource being used given that it is either in the used sample or the available sample (Johnson et al. 2006). The RSF is equal to the RSPF multiplied by an arbitrary constant, and it should be proportional to the RSPF (Manly et al. 2002, Johnson et al. 2006). Results from

studies that apply logistic regression to a use-availability design are best interpreted as a logistic discriminant function, which distinguishes between the distribution of used and the distribution of random observations rather than between used and unused (Keating and Cherry 2004, Johnson et al. 2006, Pearce and Boyce 2006). Johnson et al. (2006) argue that logistic regression results in valid relative likelihood estimates, but that variance estimates may be erroneous.

Assumptions inherent in the resource selection methods described thus far are that the availability of resources is constant and all areas are equally accessible (Arthur et al. 1996). In addition, in order for observations to be independent they must be separated by enough time for the animal to move between any 2 points in the area (Arthur et al. 1996). These assumptions may be questionable when using a random sample to estimate availability across large areas because the combinations of habitat types and other resources vary across time and space as an animal moves (Arthur et al. 1996). In order to better meet these assumptions for highly vagile animals with large home ranges, or in other situations where availability changes (e.g., seasonal vegetation die-off or sea ice melting), availability may be better represented by defining it separately for each animal location (Cooper and Millspaugh 2001). In this context, resource selection is the process by which an animal makes a choice from the set of alternatives available at a specific place and time (Alldredge and Griswold 2006). This approach is likely a better model of how animals make choices in their environment (Compton et al. 2002). However, the ability to distinguish choices and non-choices will depend on the precision and accuracy of the telemetry data. Narrowing the definition of availability reduces spatial and temporal autocorrelation associated with radiotelemetry locations, which otherwise

would result in underestimates of the variance associated with parameter estimates (Arthur et al. 1996, Garshelis 2000).

Discrete choice analysis (DCA) is one approach to analyzing data collected in this type of sampling design. The technique has been widely used in other fields but has only recently been applied to resource selection studies (McCracken et al. 1998, Cooper and Millspaugh 1999, Compton et al. 2002, Manly et al. 2002). A different conceptual design but analytically equivalent model is the 1:M or N:M matched case-control design (Breslow and Day 1980, Allison 1999, Hosmer and Lemeshow 2000, Buskirk and Millspaugh 2004, McDonald et al. 2005). DCA estimates a RSF, which gives relative probabilities of choosing a particular resource unit rather than absolute probabilities (Manly et al. 2002).

DCA addresses the problem of modeling "choice from a set of mutually exclusive and exhaustive alternatives" (Ben-Akiva and Lerman 1985). When applied to resource selection studies, the goal is to determine what characteristics of the resource choices available affect an animal's choice to use or not use those resources (Allison 1999). DCA may use any GLM appropriate for categorical responses (Hoffman and Duncan 1988), but McFadden's (1973) conditional logit model is most commonly used in resource selection studies. The conditional logit is used to determine how the characteristics of the choices available affect the likelihood of choosing a particular option by comparing choices with non-choices in terms of the explanatory variables (Breslow 1996). Each choice event is a sampling unit resulting in a dichotomous response variable to indicate whether an alternative is a choice or a non-choice (Cooper and Millspaugh 1999, Allison 1999). By considering each choice event as a stratum,

each choice is conditioned on the other choices available in the choice set (Breslow 1996). In this respect, sampling occurs conditional on the response variable (Hosmer and Lemeshow 2000).

The choice set can be defined by a radius around the location, the size of which is based on the frequency of radiolocations and prior knowledge of the species movement patterns over time, space, and different behaviors (Cooper and Millspaugh 2001). In wildlife studies, the choice set can be very large compared to human choice studies for which discrete choice models were developed (McCracken et al. 1998). In these cases it will not be feasible to enumerate the entire choice set but as a substitute a random sample may be drawn from within the defined availability radius (Cooper and Millspaugh 2001, Manly et al. 2002).

To clarify some terminology, it should be noted that the conditional logit is sometimes referred to as the multinomial logit, a term that can be broadly used to describe any model that has a response variable with more than 2 levels (So and Kuhfeld 1995). The conditional logit is a generalization of the unordered multinomial logit (McFadden 1973). The conditional logit model differs from the multinomial logit because the choice set can vary across individuals and choice events, and because the characteristics of the choices predict which alternative is selected rather than the characteristics of the chooser (Allison 1999). The multinomial model can provide information about which individuals make which choices but the conditional logit explains why those choices were made (Hoffman and Duncan 1988). Both the conditional logit and the multinomial logit reduce to the binomial logit when there are

only 2 choices and the choice set is the same across all choice events and individuals (Ben-Akiva and Lerman 1985, Allison 1999, Cooper and Millspaugh 1999).

One assumption inherent in both the multinomial and the conditional logit models for discrete choice analysis is that the odds of choosing one alternative over another are independent of the presence or absence of an unchosen third alternative independence of irrelevant alternatives, or IIA) (McFadden 1973, Ben-Akiva and Lerman 1985). Therefore, the model should be used only in situations where the alternative choices are distinct and can be weighed independently by the chooser (McFadden 1973). A large number of choices or choices that are very similar may be problematic. The IIA assumption is not important if all choice sets are the same (Allison 1999). Because of IIA, we must make the assumption that animals distinguish choices in the manner in which we have defined them and that the choices are not substitutable. The frequency of failing to meet IIA and the circumstances under which this may occur has not been addressed in the literature on animal resource selection.

STUDY AREAS

I analyzed data from 2 study areas defined by the Utah statewide cougar study (Wolfe et al. 2004): the Oquirrh Mountains in north-central Utah and Monroe Mountain in south-central Utah. Unless cited otherwise, I extracted the information below from previous documents produced as part of the statewide cougar study (Wolfe et al. 2004, Stoner 2004).

Monroe Mountain

The Monroe Mountain study area (hereafter, "Monroe") encompasses the central unit of the Fishlake National Forest (Richfield District), located southeast of Richfield, Utah, in central Piute County and southwestern Sevier County (~ 38.5° N, 112° W) (Figure 1). The mountain covers approximately 1,300 km^2 and spans 75 km north-south in the Wasatch and Uinta Mountains ecoregion (Level III), at the transition between the Colorado Plateau and the Central Basin and Range (Omernik 1987).

The topography on the site ranges from steep canyons to flat plateaus with elevations ranging from 1615 m to 3420 m. Elevations are approximately 300 m higher on Monroe Mountain than the Oquirrh Mountains but because it is a volcanic plateau, Monroe is flatter at mid to high elevations compared to the peaks and narrow ridges of the Oquirrhs. The climate in the area is hot and dry in summer and cold and snowy in winters. Temperatures and amount of precipitation varies by elevation but average monthly temperatures ranges from -4 °C in January to 20.7 °C in August (Ashcroft et al.

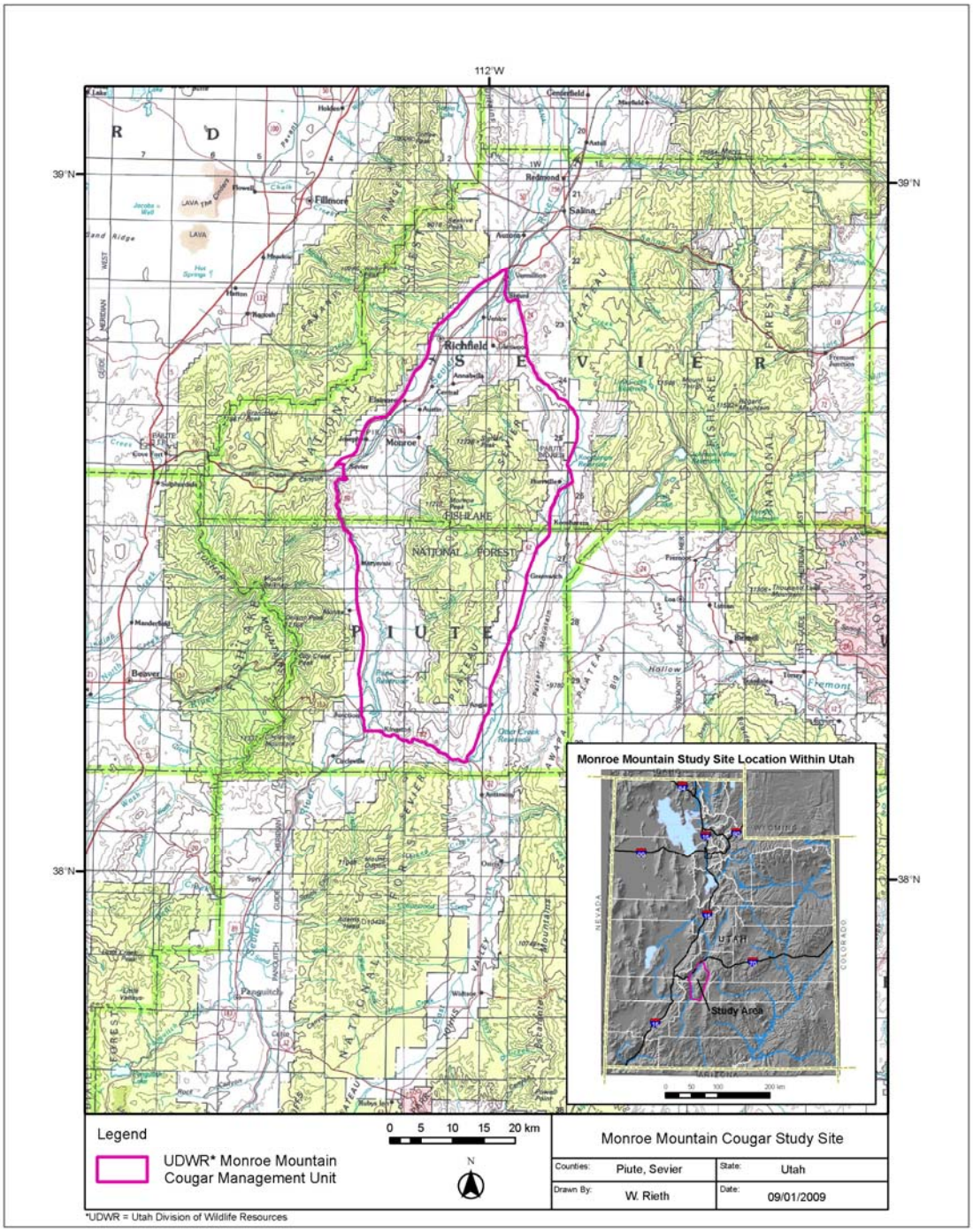

Figure 1. Map of Monroe Mountain cougar study site location

1992). Mean annual precipitation ranges from 15-20 cm in the Sevier Valley to 60-120 cm above 2,700 m, with most precipitation falling as snow (Ashcroft et al. 1992). Snow pack typically remains until mid-June above 3,000 m. Water sources on Monroe include 5 perennial creeks, 3 reservoirs, and numerous cattle tanks and springs.

The vegetation on Monroe Mountain changes with elevation but pinyon-juniper woodlands (*Pinus edulis-Juniperus scopulorum/J. osteosperma*) dominate the study area. Forests of mixed conifer (*Picea engelmannii, P. pungens, Abies lasiocarpa, Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) occur at higher elevations with patches of sub-alpine meadow interspersed among the forests. Gambel oak (*Quercus gambelii*) and other mountain shrub species (*Cercocarpus ledifolia, Rosa woodsii*) are found in patches along with mixed sagebrush (*Artemisia tridentata*)-grasslands.

Cougars on Monroe Mountain primarily prey on mule deer and elk and likely prey on a variety of other small mammals similar to the species found in the scat analysis from the Oquirrhs site (see below). In 1999 the Utah Division of Wildlife Resources estimated deer density on the Monroe Management Unit (number 23) to be 3.9 / km^2 and the density of elk was 0.5 / km^2 (UDWR, unpublished data). Two radio-collared cougars on the site killed domestic sheep (*Ovis aries*) and were removed by U.S. Department of Agriculture's Animal Damage Control program (now known as Wildlife Services). Other large to medium carnivores on the site include coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Black bears (*Ursus americanus*) were historically found on the mountain in small numbers but were not present at the time of the study.

The U.S. Forest Service manages the majority of the land on the study site but other landholders include the Bureau of Land Management (BLM), the state of Utah, and

private interests. Disturbances on the mountain include logging, livestock grazing, and heavy human recreational use by All Terrain Vehicles (ATVs). The mountain is bordered by paved roads in the valleys, including I-70 to the northeast, US-89 to the east, and state highways to the east and south. Unpaved roads and numerous ATV trails run through the canyons and up to the ridges and peaks of the mountain.

In 2003, Piute County had a population of 1,380 and a density (in 2000) of 73 people / 100 km^2; in 2003 Sevier County had a population of 19,103 and a density (in 2000) of 382 people / 100 km^2 (U.S. Census Bureau, http://quickfacts.census.gov/qfd/). Most of the human population in the area lives in small agricultural communities in the Sevier Valley to the northwest of the study site.

UDWR allows limited entry cougar sport hunting on the Monroe Management Unit. Annual cougar density estimates for adults and sub-adults on Monroe varied widely over the 9-year study period (1995-2004), ranging from 1.2 to 3.2 cougars per 100 km^2 (Wolfe et al. 2004). Seventy-four percent of the radio-collared population were hunter-killed or poached, 10% were taken for depredation control, 10% died from intraspecific strife, and 6% died of natural causes (disease, prey capture) (n=29) (Stoner 2004). Annual cougar survival on Monroe tracked harvest intensity, and varied widely from 0.36 ± 0.33 (95% CI) up to 1.0 (Stoner 2004).

Oquirrh Mountains

The Oquirrh Mountains study site (hereafter, "the Oquirrhs") is located at the southern end of the Great Salt Lake just west of the Wasatch Mountains and Salt Lake City, at the junction of Tooele, Salt Lake, and Utah counties (~ 40.5 °N, 112.2° W) (Figure 2). The

range is a 950-km^2 complex composed of the Oquirrh Mountains, which spans 55 km north-south, and the Traverse Range, which extends 27 km perpendicular to the east. The complex is on the eastern edge of the Central Basin and Range ecoregion (Level III) (Omernik 1987). The Oquirrhs and other mountain ranges in this ecoregion are characterized as forested islands surrounded by large expanses of semi-desert (Lomolino and Davis 1997, Brown 1971), where isolated mountains contain the majority of cougar habitat (Stoner 2004).

The eastern portion of the Oquirrhs consists of deep soils, rolling foothills and shallow canyons and draws. However, a high percentage of rock outcrop, steep canyons, and generally rugged topography characterize the west facing side. Elevations range from 1280 m to 3200 m. The climate is continental with the majority of the precipitation falling in the winter as snow; annual precipitation is 30-40 cm in the valleys and 100-130 cm at the highest elevations (Ashcroft et al. 1992). Temperatures range from a monthly average of –2.4 °C in January to an average of 22.2 °C in July (Ashcroft et al. 1992). Snow pack remains through mid-June above 3,000 m in some years. Water sources on the site included 2 perennial streams and numerous springs.

Gambel oak woodlands are the most common vegetation community on the Oquirrhs study area, and they occur in the foothills and lower mountain slopes. Juniper (*Juniperus osteosperma*) woodlands occur at low to mid elevations, mountain mahogany communities are found on dry, rocky ridges, and maples occur (*Acer grandidentatum*) in the canyons. Aspen and Douglas fir (*Pseudotsuga menziesii*) are found above 2,200 m, with limber pine (*Pinus flexilis*) on the ridges. Sagebrush (*Artemisia* spp.) also occurs in patches throughout the study site.

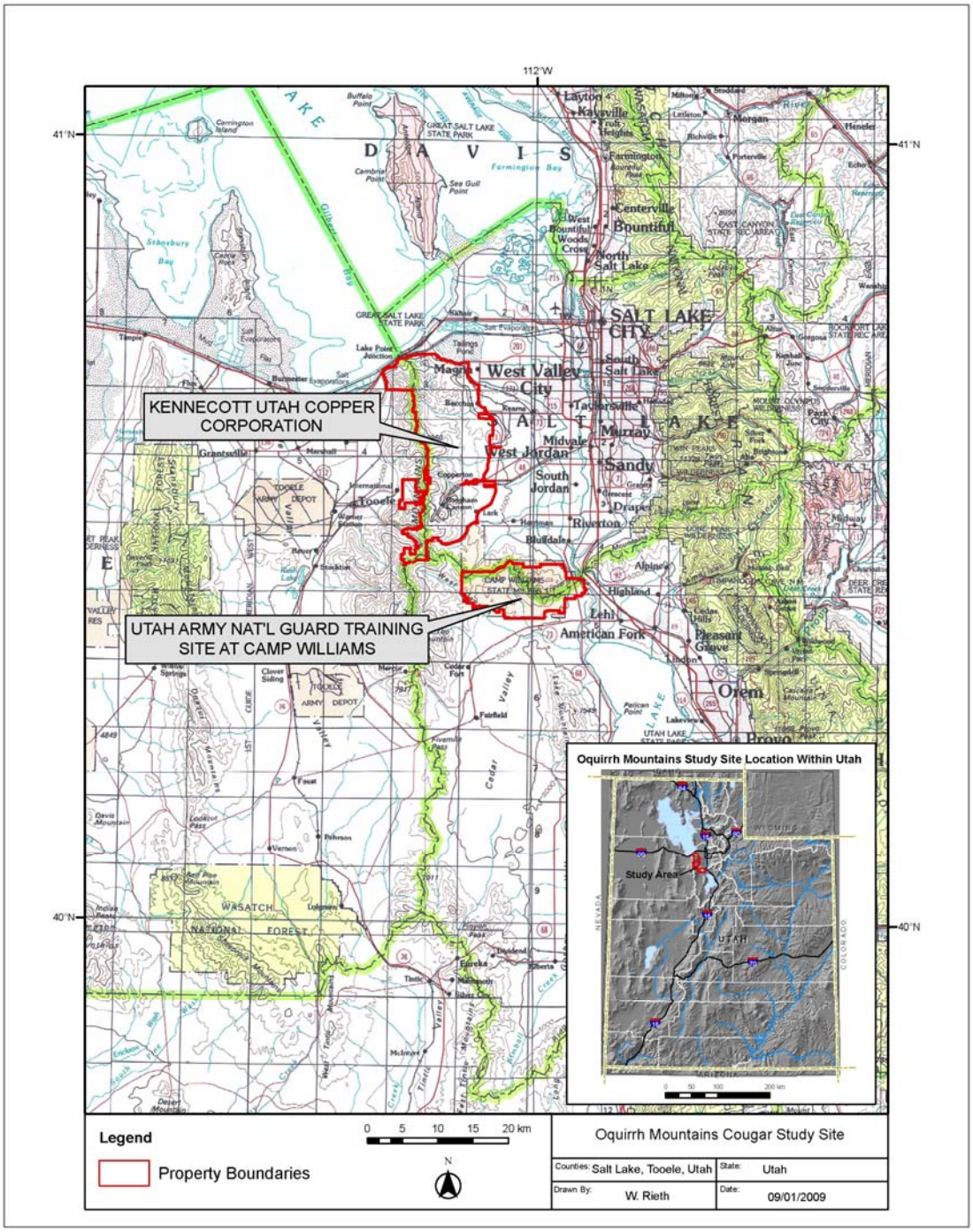

Figure 2. Map of Oquirrh Mountains cougar study site location

Cougars on the Oquirrhs primarily prey on mule deer and elk. In 1999 the Utah Division of Wildlife Resources estimated that the density of deer on the Oquirrhs-Stansbury Management Unit (number 18) was roughly 2.7 / km^2 and the density of elk was 0.2 / km^2 (UDWR, unpublished data). Note that this management unit encompasses a greater area than the site used in this study. The density of ungulates on the study site could be higher given that the 2 properties are closed to hunting. Other prey use is known from an analysis of scats collected opportunistically (Wolfe et al. 2004). Seventy-one percent of the scats contained deer and elk, or both; 34% contained small mammals, which were mostly lagomorphs and rodents but also mustelids, a porcupine (*Erithizon dorsatum*), and a felid (feral house cat (*Felis domesticus*) or juvenile bobcat (*Lynx rufus)*); birds were found in 5% of scats, and 2% contained items that could not be identified. Other predators on the site include coyotes and bobcats.

Stoner (2004) and Wolfe et al. (2004) confined the majority of cougar capture and marking efforts to the boundaries of 2 properties on the north and east side of the Oquirrhs: the Camp W. G. Williams Utah Army National Guard Training Center (hereafter, Camp Williams) (100 km^2) and the Kennecott Utah Copper Corporation property (hereafter, Kennecott) (380 km^2) (Figure 2). These 2 properties cover 60% of the Oquirrhs complex. Portions of the east and south slope of the Oquirrhs were not surveyed but are likely occupied by resident cougars. A portion of the Kennecott property has been dominated by resource extraction and industrial activities for the last 100 years. The Bingham Canyon Open Pit Copper Mine may be the largest open pit mine in the world (approximately 4 km wide, 1.2 km deep) (http://www.kennecott.com/about_facts.html). Camp Williams is located on the Traverse

Range, and training facilities consist of firing ranges for small arms, artillery firing points, and maneuver areas; training exercises in these areas result in more frequent fires than naturally occurs. The south and west sides of the Oquirrhs are owned by the BLM, cattlemen's associations, and small mining interests. Limited sheep and cattle grazing occur on the Oquirrhs. Paved roads exist on the edges of the range and around the mining operations; unpaved roads and trails exist across the range, usually in canyons. Commercial radio and television towers and their access roads mark the peaks of the range.

The highly urbanized Wasatch Front east of the Oquirrhs is densely populated and the majority of Utah's human population lives in this area. The population of Salt Lake County to the east of the Oquirrhs was 924,247 in 2003 with a density (in 2000) of 47,502 people / km^2; Utah County to the south had a population of 398,059 in 2003 and a density (in 2000) of 7,176 people / km^2. The valleys of Tooele County just west of the Oquirrhs are fairly rural; the county had a population of 47,965 in 2003 and a density (in 2000) of 230 people / km^2 (U.S. Census Bureau, http://quickfacts.census.gov/qfd/). From 1990-2000, a 30% population growth rate ranked Utah the fourth fastest growing state in the U.S. with most growth occurring in the metro areas on the Wasatch Front (http://www.censusscope.org). Based on current trends, the Oquirrh mountain range will likely be entirely surrounded by suburbs in the near future. Kennecott Land, a recently formed sister company of Kennecott Utah Copper Corporation, has begun suburban development of the eastern most portion of the Kennecott property located in South Jordan (http://www.daybreakutah.com/).

UDWR allows limited entry cougar sport hunting of cougars on the Oquirrh-Stansbury Cougar Management Unit 18. Camp Williams and Kennecott properties are closed to hunting but the remainder of the public and private land in Unit 18 is open to cougar hunting. In the last 3 years of the study, UDWR banned the taking of any cougar that wore a radio-collar, regardless of which property the animal may have been found on. Annual cougar density estimates for adults and sub-adults on the site ranged from 2.3 to 2.9 cougars / 100 km^2 but remained stable at 2.9 in 6 of the 8 years the population was monitored (Wolfe et al. 2004). Twenty-six percent of the radio-collared population were hunter-killed or poached, 5% were taken for depredation control, 16% died from intraspecific strife, 26% died of natural causes (starvation, prey capture), 11% were roadkill, and 16% had unknown causes of death (n=19) (Stoner 2004). Annual cougar survival on the Oquirrhs was fairly stable, ranging from 0.63 ± 0.28 (95% CI) up to 0.87 ± 0.23 (Stoner 2004).

The Oquirrhs study area differs from the Monroe site in at 3 major ways: (1) wildlife on the Oquirrhs are semi-protected from hunting and public access due to private land ownership, (2) a portion of the range receives intensive industrial and military use, and (3) the Oquirrhs abut suburbs near a highly urbanized, large city center.

METHODS

Telemetry

I used cougar location data to quantify and characterize cougar home ranges and resource selection. Cougars were captured, collared, and tracked on the Monroe Mountain and Oquirrh Mountains study sites as part of a larger cougar study. Wolfe et al. (2004) attempted to census the 2 populations each winter by capturing and marking all known cougars. See Stoner (2004) and Wolfe et al. (2004) for details on field methods.

I used cougar location data acquired over a 10-year period on the Oquirrhs site (1997-2007) and an 11-year period on the Monroe site (1996-2007) in the home range and resource selection analyses. On both study sites, cougars were collared with Very High Frequency (VHF) radio-transmitters manufactured by *Advanced Telemetry Solutions* (Isanti, MN). The majority of cougar locations were acquired by homing in on the collar's VHF signal with a fixed-winged aircraft. The aircraft was outfitted with a Global Positioning System (GPS) that recorded locations in Universal Transverse Mercator (UTM) coordinates. A small proportion of cougar locations were recorded using radio-tracking methods from the ground. Aerial telemetry flights were conducted approximately twice a month on each site as weather conditions permitted, typically in the morning hours between 07:00 and 12:00. Unless a collar malfunctioned, the aerial telemetry locations were acquired over the lifetime of each cougar (i.e., from date of capture to death). All analyses excluded potentially biased locations, such as capture and hunter kill sites, and any locations believed to have large errors because of a weak signal, turbulence, or high-altitude flying to avoid storms or military activity on Camp Williams.

In addition to the aerial telemetry data acquired using VHF radio-collars, resident cougars on the Oquirrhs site were also tracked using collars outfitted with GPS receivers manufactured by *Televilt* (Lindesberg, Sweden) and *Lotek* (Newmarket, Ontario). These collars provided a means of acquiring cougar location data with greater spatial accuracy and temporal coverage compared to aerial or ground telemetry methods. The GPS collars were programmed to automatically record between 5 and 8 locations across a 24-hour period, no less than 1 hour apart, and with the majority of fixes attempted during nocturnal hours when cougars were most active.

Unless otherwise noted, I conducted all statistical analyses in SAS version 9.1 and 9.2 (SAS Institute, Inc., Carey, NC) and I used ArcGIS version 9.1 and 9.3 (Environmental Systems Research Institute, Redlands, CA) for all geographic information system (GIS) analyses.

Telemetry Accuracy

In order to assess and compare the quality of the telemetry data, I estimated the spatial accuracy of the 2 types of locations (i.e., aerial radio-telemetry and GPS collar data) used in the home range and resource selection analyses. Accuracy of aerial telemetry locations was estimated by using a handheld GPS unit to ground-truth cougar mortality sites, dropped transmitters, and test collars placed on the study sites for pilots to locate. Errors were calculated as the linear distance between the aerial telemetry location and the actual location of the transmitter. There were limited data to use in assessing the errors associated with GPS collar locations because spare collars were rarely available. However, I evaluated the precision of the GPS locations by examining the variation in the

cluster of coordinates from collars that were stationary (i.e., cougar mortalities) for at least 2 weeks. I calculated this error as the linear distance between each location and the mean UTM coordinates of the point cluster, and generated a plot to examine the effect of elevation and Dilution of Precision (DOP) values (a measure of satellite geometry) on location accuracy and precision. Low DOP values indicate satellites are further apart and have wider angular separation, resulting in better geometric relationships between the satellites and the receiver and thus more accurate positions (El-Rabbany 2002).

GPS Collar Fix Rate

I calculated the fix rate of stationary GPS collars by dividing the number of locations acquired by the total number of programmed attempts. I also calculated the overall fix rates for GPS collars worn by live cougars to determine if the GPS collar data acquired from the cougars may have been biased and potentially affect home range and resource selection analyses. I summarized the number of successful and missed fixes for each cougar's collar by time of day and by season. My objective was to test for potential effects of assumed cougar activity level (moving versus resting) and amount of leaf cover, respectively, on fix rate. For the time of day variable, I categorized each GPS fix attempt into 1 of 3 diel categories (diurnal, crepuscular, and nocturnal) using annual tables of daily sunrise-sunset times for the Salt Lake City area (U.S. Naval Observatory http://aa.usno.navy.mil/data/docs/RS_OneYear.html). Following Beier et al. (1995), I defined crepuscular times as 1 hour before and after sunrise and sunset, nocturnal times as 1 hour after sunset to 1 hour before sunrise, and diurnal as 1 hour after sunrise to 1 hour before sunset. For the leaf cover variable, I used season as a surrogate under the

assumption that leaf cover would be correlated with season. I defined winter as the months of December through February, spring as March through May, summer as June through August, and fall as September through November. Where cougars had multiple years of GPS data from different collars, I pooled all years of data for an individual in each season and time of day category.

I used Cochran-Mantel-Haenszel (CMH) methods (Agresti 1996) to determine if the proportions of successful fixes were the same across all seasons and all times of day. This design considered each GPS fix event a sampling unit while adjusting for potential confounding effects of individual cougar. That is, the CMH methods were a stratified analysis of the relationship between fix rate and time of day or fix rate and season, after controlling for cougar (the strata). I first ran chi-square tests for homogeneity of proportions in the partial tables for each cougar. The response variable was fix versus no fix for 4x2 season tables and 3x2 time-of-day tables. If the patterns of association in the partial tables were in the same direction and of similar magnitude, I ran Mantel-Haenszel tests for general association to estimate the average effects of season and time of day on fix rate while adjusting for strata (e.g., individual cougar) (Agresti 1996, Stokes et al. 2000).

Some cougars had GPS collar data that covered only 2 of the 4 seasons; therefore, I repeated the CMH methods comparing only the winter and spring seasons. Because the 2-season tables were 2x2 I estimated effect size using odds ratios. Odd ratios are used to compare the likelihood of an event (e.g., GPS fix) occurring in 2 different groups (e.g., winter versus spring seasons). The odds of an event occurring in one group is the probability the event will occur divided by the probability the event will not occur. To

compare the odds for 2 groups, the odds ratio is then calculated by dividing the odds of an event occurring in one group by the odds of the event occurring in another group. An odds ratio less than 1 indicates the event is less likely in one group compared to the second group whereas an odds ratio greater than 1 indicates the event is more likely. An odds ratio equal to 1 indicates the event is equally likely in both groups.

I conducted a Breslow-Day test for homogeneity of the odds ratios across cougars in the 2x2 season tables. If the odds ratios were homogenous, I conducted a Mantel-Haenszel test for average seasonal effects across strata and calculated a common odds ratio (Agresti 1996). For both the season and time of day partial tables, I calculated cell chi-square values to determine which cells showed the greatest difference from their expected value, contributing the most to the overall chi-square value.

Home Range Estimation

I estimated cougar home ranges in 2 phases. First, I used aerial telemetry data to estimate multi-year diurnal home ranges for both the Monroe Mountain and Oquirrh Mountains study sites in order to compare results from the 2 sites and to other cougar studies. Second, I estimated home ranges for cougars at the Oquirrhs site using exclusively GPS collar data. The purpose of the second phase of analysis was to evaluate cougar space use over shorter temporal scales (e.g., yearly, seasonally, monthly), the impact of using a finer sampling interval, and the importance of including nocturnal data when estimating cougar home ranges.

Multi-year Diurnal Home Ranges from Aerial Telemetry

I estimated multi-year home ranges at both study sites using aerial telemetry locations for cougars that had approximately 30 locations or more (Seaman et al. 1999, Kernohan et al. 2001). Any aerial or ground location taken within 24 hours of another location was excluded to avoid spatial and temporal autocorrelation. For cougars on the Oquirrhs that were tracked with both aerial telemetry and GPS collars I report 2 diurnal home range estimates: one estimated from the aerial telemetry data exclusively and one estimated from both a.m. diurnal GPS and aerial telemetry data. I generated 2 home range estimates because the aerial telemetry sample sizes were limited for many cougars. This necessitated supplementing aerial telemetry data with locations from the GPS dataset in order to increase the number of locations per cougar and the total number of cougars used in both the home range analysis and the resource selection analysis (which required delineation of a home range). I used a single a.m. diurnal reading per day (between 07:00 and 12:00) from the GPS datasets to ensure the locations represented the same time period as the aerial locations. When a diurnal aerial telemetry location and an a.m. GPS collar location were acquired on the same day I used the GPS location because of the greater spatial accuracy.

Any clustering in the diurnal GPS data was removed prior to estimating a home range. That is, if a cougar had consecutive GPS locations clustered together over multiple days (e.g., due to a prey cache, natal den, or repeated use of a daybed site), I used the average of the coordinates in the cluster. I identified clusters in the GPS data by generating monthly point distributions and movement paths and stepping through

locations sequentially while viewing the data over aerial photographs for context. I considered clusters to be 2 or more locations within 200 m of each other within a 48-hour period (Anderson and Lindzey 2003).

By including the diurnal GPS data, I was able to add 5 additional female and 2 additional male cougars to the analysis for the Oquirrhs site than would have been possible with the aerial telemetry dataset alone. The home range analyses included both male and female cougars on the Oquirrhs site. Only female cougars were included in the analysis for Monroe because there were no male cougars from the site that had at least 30 locations.

I used the Animal Movement Analysis Extension (Hooge and Eichenlaub 2000) in ESRI's ArcView 3.x to generate fixed kernel (FK) density and minimum convex polygon (MCP) home ranges from the diurnal telemetry data. For the FK home ranges, I selected the smoothing factor (i.e., h-value) via least squares cross-validation (LSCV) (Seaman et al. 1999, Kernohan et al. 2001), and calculated the area within the 95% probability volume contours. I calculated the MCP home ranges for comparability with previous cougar studies that had similar sample sizes (Harris et al. 1990, Garton et al. 2001). Research indicates that the fixed kernel algorithm is the most reliable of current home range estimation methods (Powell 2000). Using the 95% contour as opposed to the 100% contour eliminates extreme locations, which may be considered "occasional sallies" (Burt 1943). These distant locations may not be reliable or repeatable from a statistical stand point (Powell 2000). Furthermore, the 95% contour is most commonly reported in the literature (Powell 2000), thus using this method allows comparability of estimates among different studies. Maps were generated to examine home range overlap

with other cougars, possible influences on home range boundaries, and other features of the landscape that could affect cougar space use.

None of the few visually obvious outliers were removed because they were determined to be valid cougar locations representing cougar space use over multiple years. In addition, these locations did not appear to substantially increase the estimated area nor did they add large, unused sections to the delineated home range. The MCP estimation method would be more sensitive to potential outliers than the FK method.

To determine if a minimum sample size of 30 locations was adequate for delineating home ranges (Harris et al. 1990, Kernohan 2001) I conducted asymptote analyses on MCP home ranges using the program ABODE (beta, v.3) for ArcGIS (Laver 2005). ABODE calculates home range area over various sample sizes by first generating an initial MCP with 3 locations selected from the dataset, then generating a new MCP with each additional location. The majority of the diurnal telemetry data were collected at a relatively irregular sampling interval; therefore, locations were added to the asymptote analysis in random rather than consecutive order (Harris et al. 1990). Because the random approach incorporates stochasticity, I added a looping procedure to ABODE using Visual Basic, which repeated the asymptote analysis 500 times for each cougar home range. I calculated the mean area for the 500 iterations at each sample size and the percent change in area with each additional point. I identified an asymptote as the number of locations at which an additional location added less than 1% to the area or where the last 10 locations added less than 10% (Odum and Kuenzler 1955). I used linear regression to determine if there was a relationship between sample size and estimates of home range size.

Annual Home Ranges from GPS Collar Data

In the second phase of the home range analysis, I calculated annual FK and MCP home ranges for cougars on the Oquirrhs site exclusively with the GPS collar data, and using locations from all times of day. I used the same FK and MCP estimation methods that were used to estimate the multi-year diurnal home ranges. In order to maintain a consistent sampling interval, I did not remove any clustered locations. However, even when clustering around daybed or cache sites was removed from the GPS data, additional clumping across larger time intervals remained and caused the LSCV method of selecting an h-value to fail (Hemson et al. 2005). Therefore, to select a smoothing factor for the FK home ranges I began with the h-value set at 100 m and increased the value incrementally by 100 m until the polygon was contiguous (Kie and Ager 2005). Due to the lengthy computation time required for the large sample sizes, I did not calculate MCP home range asymptotes with the complete GPS datasets. I assumed the large sample sizes were adequate for delineating home ranges.

In addition to annual home ranges, I also calculated monthly and seasonal (seasons as defined as above in the GPS fix-rate analysis) home ranges from the GPS data using the MCP method to determine what percentage of the annual home range was used each month and to evaluate any seasonal differences in home range size. Due to spatial and temporal autocorrelation in the cache site clusters, the number of GPS locations was insufficient to generate monthly or seasonal home ranges using FK methods. I also calculated nocturnal (included crepuscular locations) and diurnal MCP and FK annual home ranges to determine if acquiring locations over different times of day affected the home range estimates.

Resource Selection

I examined cougar resource selection in 2 phases: (1) a coarse-scale characterization of diurnal resource selection on both the Monroe Mountain and Oquirrh Mountains study sites using aerial telemetry data, and (2) a fine scale analysis using GPS collar data from cougars on the Oquirrh Mountains to investigate resource selection decisions made at finer temporal and spatial scales and over various behaviors.

Coarse Level: Diurnal Use Versus Availability

For the coarse-level analysis, I used cougar telemetry data to quantify diurnal resource selection on the Oquirrhs and Monroe study sites. This phase of the study was conducted under the hierarchical framework of resource selection defined by Johnson (1980). I examined second-order selection (home range selection versus study area) and third-order selection (use within home range) to determine if cougar resource use was disproportionate to availability at either scale. First and fourth-order selection were not included in this analysis since the available cougar data were not appropriately analyzed at these scales.

My sample for the coarse level resource selection analysis was restricted to cougars with at least 30 diurnal locations so that a home range could be delineated. In order to increase number of locations per cougar as well as the total number of cougars used in the analyses, I supplemented aerial and ground telemetry data with locations from the GPS dataset (as discussed in the home range section). This applied only to cougars that wore GPS collars on the Oquirrhs site. Any clustering in the diurnal GPS data was removed as described in the home range section.

The study site boundaries were delineated as a 95% volume FK contour around all cougar locations used in the coarse level analysis (Figure 3, Figure 4). I selected the smoothing factor for this FK contour by using the largest LSCV value from the individual cougar home range data, and increasing this by 100 m until the boundary was no longer separated into disjointed areas. Using a MCP around all locations to delineate the study site boundary would have included a large area where there was no information on cougar presence or resource use (i.e., on the west and south slopes of the Oquirrh Mountains). Cougar home range boundaries were defined in the resource selection analyses as the 95% volume contour on the FK estimates. Using the 95% contour eliminated locations with lowest probability of use, and thus was a better representation of overall cougar resource use at this scale. Seaman et al. (1999) recommended that peripheral areas of the home range receive less focus in habitat selection studies. Using a contour smaller than 95% (e.g., 85%) would have reduced the sample size for the third-order analysis to an unacceptable level for some individuals since a larger portion of their radiotelemetry locations would have been excluded. For cougars with both GPS and aerial telemetry locations, I used the FK home range delineated from the combined datasets as described in the section above on home range analysis.

I quantified second-order cougar resource selection on each study site with respect to land cover types, edge density, slope classes, and landform. I quantified third-order selection on each site with respect to land cover types, slope, and landform. The relatively poor accuracy of the aerial telemetry locations and coarse resolution of the land cover data precluded analysis of edge use at third-order selection.

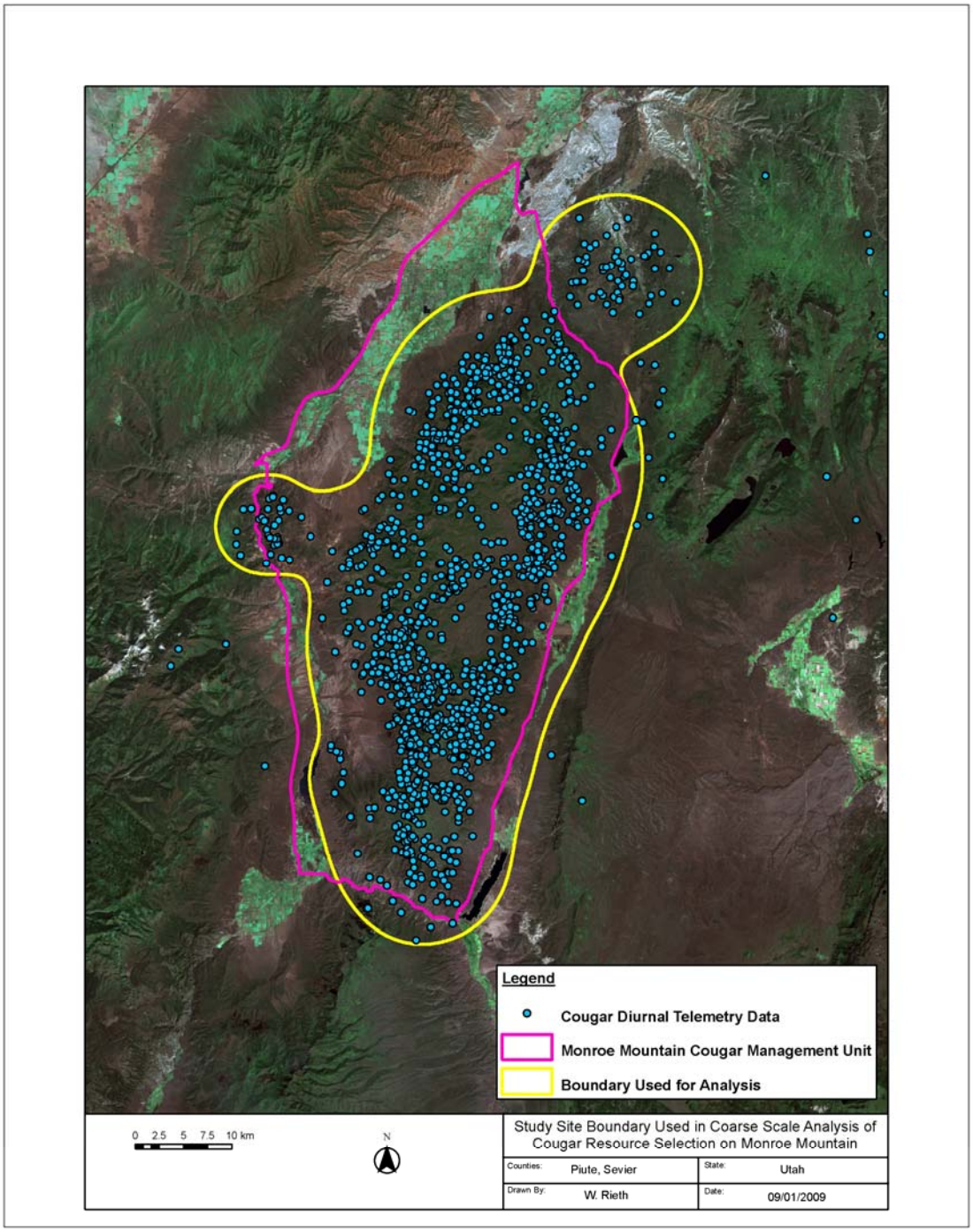

Figure 3. Map of study site boundary used in coarse scale analysis of cougar resource selection on Monroe Mountain, Utah.

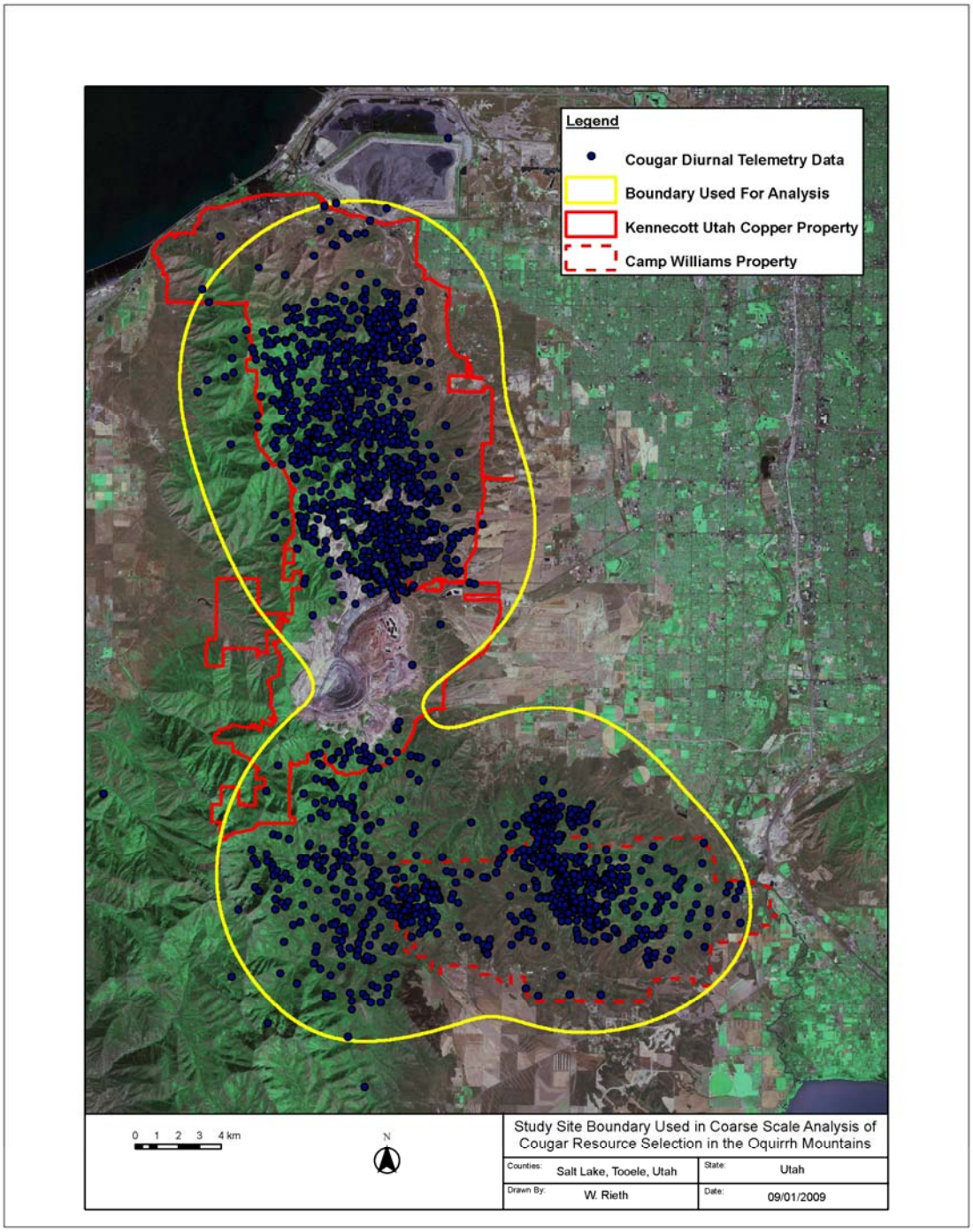

Figure 4. Map of study site boundary used in coarse scale analysis of cougar resource selection in the Oquirrh Mountains, Utah.

I extracted information on land cover types in the study areas from the Southwest Regional Gap Analysis Project (SWReGAP) map (USGS 2004). SWReGAP used decision tree classifiers to model land cover from field data, ancillary data layers, and 30-m Landsat-7 Enhanced Thematic Mapper imagery acquired between 1999-2001 (Lowry et al. 2005). The land cover map units were ecological systems that were developed by NatureServe™ as a component of the International Terrestrial Ecological Systems Classification (Comer et al. 2003). The minimum mapping unit was 0.45 ha. See Lowry et al. (2005) for further details on land cover mapping methods. I reclassified the SWReGAP cover types on each study site by aggregating types that were rare and/or ecologically similar into fewer classes based on structure, under-story characteristics, elevation range, and relative abundance on each study site (Table A.1 and Table A.2 in Appendix A). This resulted in 12 cover types for use in the resource selection analyses: cliff and rock, coniferous forest, deciduous forest, deciduous woodland, coniferous woodland, montane shrubland, basin shrubland, grassland, riparian, agriculture, disturbed, and developed. I ignored the open water class in all analyses. Aggregation of cover types likely improved the classification accuracy of the land cover data. Land cover maps of the reclassified cover types on both study sites are included in Figure B.1 and Figure B.2 in Appendix B.

I used the Extract Edge tool in Hawth's Analysis Tools for ArcGIS (Beyer 2004) to extract edge values from the reclassified SWReGAP land cover map. I calculated edge density using a 1,000-m moving window, which approximated the combined mean male and female LSCV values that were used as smoothing values when estimating the FK home ranges at both study sites.

I generated a slope raster layer for each study site from a 30-m U.S. Geological Survey (USGS) Digital Elevation Model (DEM) and classified grid cells into 4 bins based on those used in a previous cougar study (Logan and Irwin 1985): gentle (<20% slope), moderate (20-40%), steep (40-70%), and rugged (70-100%). I used a topographic position index (TPI) extension for ArcView 3.x (Jenness 2005) to generate TPIs and a landform model for each study site. The TPI calculated the difference between the elevation of a grid cell and the elevation of cells in the surrounding neighborhood of specified width. I used the ArcView TPI extension to generate a 10-class landform model using slope, a large-neighborhood TPI (2000 m) and a small-neighborhood TPI (500 m). This approach made it possible to distinguish valley bottoms occurring between mountain ranges from canyons within the mountain range. I aggregated the 10 class output into a 5-class model: canyons/drainages, steep slopes, valley bottoms/mesas, gentle slopes, and ridges/hilltops (Table C.1 in Appendix C).

For the second-order analysis of cougar resource selection, I compared resources within a home range (use) to resources in the study area (availability). I estimated the availability of resources on each study site by randomly placing 1,000 simulated circular home ranges within the study site boundary and calculating the proportion of resources (or mean for continuous variables) within each simulated home range polygon (Wilson et al. 1998, Katnik and Wilegus 2005). A circular area was used for the simulation because the shape better fit within the study area's rounded boundaries compared to other shapes, such as a square. I quantified availability of resources separately for sex and study site (i.e., male cougars on the Oquirrhs, females on the Oquirrhs, and females on Monroe),

where the size of the simulated home range was equal to the mean home range size for each group.

Cougar use of each resource type at the second order was defined as the proportion (or mean) of that resource within each cougar's 95% FK home range. Cougar home ranges that extended outside the analysis boundary were clipped to the boundary prior to analysis. I conducted the GIS procedures for the random home range simulations using a combination of Hawth's Tools, Arc Macro Language (AML) scripting, and Python scripting. I used a Kolmogorov-Smirnov (K-S) goodness-of-fit test (Zar 1999) to compare a Cumulative Distribution Function (CDF) of proportions of land cover, slope, and landform resources generated from cougar home ranges to a CDF generated from the random home ranges (Katnik and Wielgus 2005). For edge density, I compared the mean values from random versus cougar home ranges. The K-S test is a non-parametric and distribution free test that is used to determine if 2 datasets differ (Zar 1999). While the t-test is potentially a more powerful test than K-S, in some cases it may not give valid results. For example, if the means of 2 dataset do not differ (e.g., because both are centered around or near the same value), but the ranges of the distributions differ (i.e., there is actually more variation in one group) the t-test results would incorrectly indicate that the 2 distributions were not different.

For the categorical variables (vegetation type, slope class, landform) individual statistical tests were run on each level of the variable (i.e., on each of the 12 land cover types). Because multiple hypotheses were tested for categorical variables (e.g., one hypothesis was tested for each vegetation type), there was an increased potential for Type I errors. To account for this possibility, I used multiple comparison procedures to control

for false discovery rate (FDR) (Benjamini and Hochberg 1995, Garcia 2004, Verhoeven et al. 2005). FDR methods control for the expected proportion of erroneously rejected null hypotheses (i.e., the false positive rate) among all tests that are significant.

For the third-order analysis of resource selection, I compared use of resources (as measured at cougar telemetry locations) to availability of resources within the cougar's home range. Any location that fell outside the home range boundary was excluded. As with the home range analysis, if the GPS data indicated that the cougar was on a cache, I used the mean location of point clusters in place of the clustered locations to reduce spatial and temporal autocorrelation.

I buffered telemetry locations by a measure of their associated spatial error (aerial = 500 m, GPS = 100 m). Using polygons around locations rather than points in habitat analyses accounts for the accuracy and precision of telemetry locations, land cover classification errors, and also characterizes the context and configuration of patch types surrounding the point (Rettie and McLoughlin 1999). The grid cells representing resources within the buffered radiolocations were autocorrelated and would have resulted in a misleadingly large sample size if the number of cells of each resource type were used as the observed counts (use). Therefore I calculated observed counts in each resource category (e.g., vegetation type) by taking the proportion of resource types within each buffer, summing these proportions for each type across all buffers within an animal, and rounding to the nearest integer. When calculated in this manner, a cougar's sample size for the observed counts was equal to the number of radiolocations for that animal. When all buffer sizes were the same within an animal, this calculation was equivalent to the method suggested by Wickens (1989), which accounts for dependence in grouped

observations by dividing the chi-squared value by the number of groups (in this case, the total number of grid cells summed over all buffers) to get a test statistic. Two buffer sizes were used for an individual if a cougar had both aerial telemetry and GPS collar locations. This method of calculating observed counts maintains the higher precision associated with the GPS collar data. I extracted GIS data for each resource within the buffers using Hawth's tools and AML scripting, and I calculated proportions within the buffers using Python scripting. Expected counts (availability) were calculated by multiplying the proportion of each resource type in the home range by the number of radiolocations for the cougar (White and Garrott 1990).

To determine if cougars used resources selectively at the third order, I conducted 1-way chi-squared goodness-of-fit tests on each cougar to determine if the individual used resources in proportion to availability (White and Garrott 1990, Manly et al. 2002). In order to minimize the number of cells in the contingency table with zeroes and expected counts less than 5 for the vegetation data, I further combined or dropped rare types from the 12-class land cover data (Manly et al. 2002). I dropped grassland, riparian, agriculture, disturbed, and developed land cover types since the majority of cougar radiolocations observed and expected in these cover types were less than 5. These types were either rare or cougars had previously excluded them at the second order of selection when they selected a home range. Additionally, I combined basin shrublands and montane shrublands into 1 class because the break between these types was predominantly based on elevation in the SWReGAP map. Otherwise they were similar in structure and shrub density on the study sites, being mostly composed of sagebrush. This resulted in testing for the 5 most common land cover types in the third-order analysis:

coniferous forest, deciduous forest, coniferous woodland, deciduous woodland, and shrubland.

For the third-order analyses, I summed the chi-squared values and degrees of freedom from the individual cougar tests for an overall test of selection by the population (White and Garrott 1990, Manly et al. 2002). Asymptotic chi-square tests may not give accurate results when cells are sparse or unbalanced, or the overall sample size is small (Agresti 1996, Stokes et al. 2000). Therefore, when contingency tables were still sparse (i.e., at least 1 cell contained expected counts ≤ 5) after dropping and combining categories, I conducted exact 1-way chi-square tests rather than calculating the asymptotic Pearson or log-likelihood statistic. Otherwise, if data were sufficient, I used the Pearson statistic since this was an observational study (Stokes et al. 2000).

To estimate the selection probability for each of level of the resource variables (e.g., vegetation type), I calculated standardized selection ratios and confidence intervals for each type using a Bonferroni correction (Manly et al. 2002). The Bonferroni correction was necessary because multiple individual hypotheses were being tested within a family (i.e., 1 test for each vegetation type), which increases the probability of a Type I error over all the tests (Manly et al. 2002). To compensate for this, the Bonferroni correction adjusts p-values and confidence intervals such that a stronger level of evidence is required to draw inferences. The correction results in conservative (wide) confidence intervals (Manly et al. 2002). For an overall test, I averaged the selection ratios for each type across all cougars (Manly et al. 2002).

Fine Level: Modeling Selection During Different Behaviors

Model Development.— In the fine-scale modeling of cougar resource selection, I used GPS collar data from 9 female and 3 male cougars on the Oquirrhs study site. The goal of the modeling was to determine which environmental variables affected cougar's choice to use a particular site for a particular behavior. I generated models for 3 types of cougar behaviors that were discernable with the GPS data: prey caching, resting at a daybed, and hunting. Natal denning was also of interest, but the small sample size precluded formal analysis. I also examined 2 scales or spatial extents for resource availability: the home range scale (i.e., used locations versus availability in home range) and the discrete choice scale, which modeled choices made by cougars within a limited time frame and area. Both of these scales are akin to Johnson's (1980) fourth-order selection because the data represent cougar selection of a particular patch during a specific behavior or activity. Six resource selection models were considered (3 behaviors x 2 scales).

Caching behavior was identified as a site with multiple telemetry locations within 200 m of each other over 2 or more nights (Beier et al. 1995, Anderson and Lindzey 2003). I used the mean of the cluster of these locations as the chosen cache site. I defined daybed sites as any diurnal location that was not a cache site. Hunting was identified as any location used during nocturnal and crespuscular hours that was not previously identified as a cache site (Beier et al. 1995). If multiple diurnal locations were within 200 m of each other during the same day or over consecutive days, I used the mean of the point cluster. Similarly, if nocturnal locations were clustered over several

consecutive hours (but not more than 1 night, which would indicate a cache site) I used the mean of the cluster. See the previous section on home range estimation for techniques used to identify point clusters.

In order to maximize battery life, GPS collars were programmed to attempt the majority of fixes during hours of greatest cougar activity. For this reason, there was a greater sample of used locations for nocturnal and crepuscular activities than the other 3 activities. In addition, multiple clustered points were more frequent in diurnal and caching behaviors than in nocturnal activities, and replacing these clusters with single points to minimize autocorrelation further reduced the sample size.

I used all non-clustered cougar cache locations and daybed locations in the models. However, because the number of nocturnal and crepuscular locations was extremely large (more than 10,000), I used only 1 location per night. I randomly selected 1 nocturnal or crespucular location out of the set of locations available for each nighttime period (between 1 hour before sunset and 1 hour after sunrise). This subsampling minimized temporal and spatial autocorrelation effects and reduced the amount of labor required for measuring environment variables.

I used matched conditional logistic regression for all 6 models considered in the fine-level analysis of cougar resource selection. I matched 1 chosen location to 5 random locations within each choice set defined by the sampling domain. At the home range scale, I defined the choice set as used and available locations within a cougar home range and matching was on individual cougar. That is, 5 times as many random locations as used locations were identified within each cougar's home range. At the discrete choice scale, I defined the choice set as circle with a 200-m radius around a cougar location.

This radius of perception was based on literature that indicated that this may be the maximum distance that a cougar would consider when making choices about where to cache prey (Beier et al. 1995, Laundre and Hernandez 2003). This distance was also applied to locations defined as daybed and nocturnal use sites. From a statistical standpoint, it was necessary to use a radius that was large enough to capture enough environmental variation to be able to distinguish differences, particularly for continuous variables like elevation. However, a very large radius would not capture discrete decisions made at fine temporal and spatial scales. Furthermore, as the size of the choice radius increases, the discrete choice model would approach the home range scale models. Some studies (e.g., Arthur et al. 1996) have defined the choice radius based on time and distance between consecutive locations. However, because the sampling interval was not fixed in this study (due to differences in collar fix rate) and because nocturnal locations were randomly subsampled, this was not a feasible method. In addition, the distance between consecutive daybed sites and cache sites would have been large. The home range scale models were included in order to model cougar resource selection over these larger spatial extents.

I used the Conditional Point Sampling Tool in Hawth's Tools for ArcGIS (Beyer 2004) to generate 5 random locations within the sampling domain defined for each of the 2 scales (i.e., within the home range for or within 200-m radius of used location). Explanatory variables listed in Table 1 were measured for each chosen location and the matched random locations. These variables were selected based on prior studies of cougar habitat and mule deer or elk habitat. Quadratic forms of slope and elevation were included to represent possible curvilinear relationships between these variables and

cougar use. That is, cougars may favor an optimal range of values for these variables (e.g., slopes that are not too steep but not too gentle). Further information on measurement of explanatory variables is given below.

Table 1. Explanatory variables used in matched conditional logistic regression models for cougar resource selection in the Oquirrh Mountains, Utah, USA.

Variable (abbreviation)	Type (levels)	Data source
Land cover (LC)	Categorical (10)	Aerial photo interpretation
Elevation (ELEV) & elevation^2 (ELEVSQ)	Continuous	DEM
Aspect (ASP)	Categorical (4)	Derived from DEM
Land cover diversity (DIV)	Categorical	Derived from SWReGAP
Landform (LF)	Categorical (5)	Derived from DEM
Slope (SLP) & slope^2 (ELEVSQ)	Continuous	Derived from DEM
Standard deviation of slope (SDSLP)	Continuous	Derived from slope
Distance to stream (STRM)	Continuous	DLG 1:100K USGS quad
Distance to roads (ROADS)	Continuous	DLG 1:24K USGS quad
Edge (EDGE)	Categorical (2)	Aerial photo interpretation

Assessing finer scale decisions in resource selection requires more accurate telemetry data as well as finer data on resources (Rettie and McLoughlin 1999). The SWReGAP land cover map was not resolute enough to identify fine-scale patterns (e.g., vegetation patches) that would likely be discernable to cougars. In order to match the scale (grain) of the telemetry data to the land cover data, I assigned a cover type using aerial photo-interpretation. Ten land cover types were used as the classification scheme for the aerial photo interpretation: cliff/rock, coniferous forest, deciduous forest, deciduous woodland, coniferous woodland, shrubland, grassland, riparian, agriculture, and disturbed/developed. I used high resolution color ortho-imagery (0.3-m resolution)

acquired in 2003 for the east side of the range. Elsewhere I used 1-m color imagery from the National Agricultural Imagery Program acquired in 2004, and 1-m black and white Digital Orthophoto Quads acquired in 1997 (Utah AGRC http://agrc.utah.gov/index.html). All photo interpretation was conducted "blindly"; that is, points were in random order and I did not know if a particular point was a used location or a random location at the time I assigned a land cover type to that point. One disadvantage of using this technique to measure resources more precisely was that I was not able to produce a spatially-explicit model.

Land cover diversity was computed from SWReGAP data using the Focal Variety Tool in ArcGIS, which uses a moving window to calculate the number of land cover types within a specified neighborhood. I used a 3x3 rectangular neighborhood.

I extracted edge information using GIS and "blind" aerial photo-interpretation. To examine edge effects, I used a binary variable (edge versus no edge). Cougar locations and random locations were buffered by 25 m, and viewed over the aerial photographs in ArcGIS. If the location's 25-m buffer encompassed an edge, a 1 was assigned to that location to represent edge; otherwise the location was assigned a zero to indicate that it was not on an edge (Laundre and Hernandez 2003). Edge was defined to be where overstory cover was adjacent to open cover types. I considered woodland and forest vegetation to be cover, and shrublands, grass, and disturbed/developed types to be open areas. Note that this is a different definition of edge than that used in the second-order selection analysis, which calculated edge between all land cover types regardless of structure.

Sources of data for the other variables considered are listed in Table 1. Derivation of the landform layer is described above in the section on coarse-scale resource selection. I used 4 categories for aspect: North=315-45, East=45-135, South=135-225, and West=225-315. Standard deviation of slope was included as an index of terrain ruggedness.

I included distance to streams because deer and cougars have been attracted to these areas in other studies (Logan and Sweanor 2001, Dickson and Beier 2002). Both the riparian land cover type and distance to stream variables were included in modeling efforts because not all streams in the Oquirrh Mountains are characterized by riparian vegetation.

Continuous variables were centered in SAS prior to creating higher order terms and prior to running through the model. Centering was achieved by subtracting the average of each variable from every value of that variable in the dataset. This rescaled the data so that statistical testing occurred within the range of the data rather than extrapolating out to other values. Centering maintains the variable distribution centered on the observed mean rather than on zero, which is particularly important when there are no meaningful zero values in the data (Aiken and West 1991). For example, there were no elevation values of zero in the study area. Centering also reduces any collinearity among explanatory variables (particularly in higher ordered terms) (Aiken and West 1991).

Prior to formulating models, I examined standard diagnostic statistics for multicollinearity using PROC REG in SAS. I first examined condition indices, which may be used to assess collinearity in more than 2 variables. Statistical software

calculates these indices by decomposing a correlation matrix into a linear combination of the explanatory variables and finding the eigen values, which are the variances of each linear combination (Freund and Littell 2000). Condition indices are a function of the eigen values. Condition indices between 10 and 30 indicate moderate dependencies among variables that may affect parameter estimates. Condition indices > 30 indicate strong collinearity (Belsley et al. 2004). If any condition index was greater than 10, I then examined the Variance Inflation Factor (VIF). VIF greater than 2.5 may indicate the presence of collinearity (Allison 1999). If a variable was collinear with any other variable, it was removed from consideration in any model. Multicollinearity may result in instable parameter estimates and large standard errors around the parameter estimates (βs) but does not affect goodness of fit tests for the overall model (Allison 1999).

A priori, I generated a set of approximately 20 candidate models for each behavior and scale of interest. The models included various combinations of the variables described above, and were based on hypotheses I formulated about cougar use of particular resources for different behaviors. In general, I included fewer continuous variables in the discrete choice scale models because the sampling within the choice set domain occurred over a small extent, which reduces the variance compared to the home range extent. For example, I would not expect cougars to selectively use elevation given choices available in a localized area but they may select certain elevations given the choices available across their entire home range.

I hypothesized that cougars would select cache sites that provide protection of the carcass from scavengers, other cougars, and spoilage, that minimize the energy required to drag the carcass from the kill site, that were associated with areas that deer may favor,

or that were located away from human disturbance. Models were produced from single hypotheses (e.g., spoilage) as well as various combinations of these hypotheses by cross walking the hypotheses to the variables described above. For example, cougars likely hide carcasses through the use of vegetative cover (land cover) and topographic cover (landform). Spoilage could be prevented through the use of particular aspects, landforms, and vegetation types that provide reduced ambient temperatures. Minimization of energy expenditure could be a response to landform, slope, ruggedness (SD slope), and elevation. Because cougars drag carcasses a relatively short distance, cache sites may reflect areas that deer prefer or where deer are most easily killed, and this could be indexed with the aspect, land cover diversity, distance to streams, edge, elevation, and vegetation variables.

I hypothesized that cougars would select daybed sites that provide hiding cover, protection from precipitation, and optimize thermoregulation, and that factors related to prey use or energy expenditure would have less of an influence on cougar daybed selection. For cougar hunting activities (nocturnal use), I hypothesized that cougars would select sites that minimize energy expenditure, are highly used by prey, provide stalking cover, or are otherwise advantageous to cougar kill success. Models were generated for daybed and nocturnal use in a similar manner as described above for cache site models.

The model set always included the global (or saturated) model (Burnham and Anderson 2002). All models included the land cover variable because vegetation is the most prominent feature on the landscape and is likely the primary driver of cougar use of an area for a particular activity. Burnham and Anderson (2002) refer to this as a

"dominant variable". To verify that land cover was a dominant variable, I also included the global model with the land cover variable omitted. Models that included quadratic variables always included the lower order term in order to avoid confounding linear and quadratic variance. According to the hierarchy principle of model building, higher order terms can only be interpreted when the lower order terms are included in the model (Collett 2003).

After identifying the initial set of candidate models, I input the global model through conditional matched logistic regression and identified variables that were statistically significant at alpha=0.05. All variables that were significant at this level were used to generate 1 additional model to add to the candidate list if it was not already included. In 2 of the 6 cases, the model was already included on the candidate list.

I estimated matched conditional logistic regression models for all candidate models in the sets that were defined a priori using PROC LOGISTIC in SAS. I pooled data across all cougars, but individual effects were controlled at both scales by the matching variable (i.e., the strata). The use locations were matched to random locations using the STRATA statement in PROC LOGISTIC. For the home range scale models, the stratum was cougar ID. This was an *N*: *M* matched design where multiple used points were matched to multiple random points within a cougar home range, but maintained a 1:5 ratio (5 times as many random locations as used locations). For the discrete choice models, the stratum was the choice set. This was a 1: *M* matched design where 1 used point was matched to 5 random points.

Model Selection. – The set of candidate models was evaluated from the set of the alternative models using Akaike Information Criteria (AIC) (Burnham and Anderson

2002). I first examined the fit of the global model using a likelihood-ratio test. If the global model fit well, then this indicated that any more parsimonious model in the candidate set would also fit the data. If the global model fit poorly, AIC would have selected the best model out of a set of poor fitting models (Burnham and Anderson 2002).

Because AIC values are on a relative scale their absolute value is not important. AIC values are only comparable to other AIC values in the same model set. In order to compare candidate models I calculated the differences in AIC values (ΔAIC) by ordering the models in a set from smallest to largest AIC, and subtracting each model's AIC value from the smallest AIC value among the candidate models (Burnham and Anderson 2002). Any model with ΔAIC within 2 to 4 units of the top model was considered equally well at approximating the data, and models with ΔAIC greater than 10 had essentially no support (Burnham and Anderson 2002). Due to the tendency of AIC methods to overfit data (Burnham and Anderson 2002), I selected the most parsimonious model (i.e., fewest variables) as the "best" model out of the top ranked models if there was more than 1 top model. Furthermore, Burnham and Anderson (2002) suggest that where models have ΔAIC within 2 units of the best model, differ by only 1 parameter, and have approximately the same maximized log-likelihood value, the larger models (i.e., more parameters) are not competitive with the top model because the model fit is not improved based on the log-likelihood value. Selecting the most parsimonious model ensures precise estimates of model parameters and a more general application of model results. The "best" model was used to interpret coefficients and make inferences, and was also used in the cross-validation procedures.

I used AIC_c instead of AIC to correct for small sample size if the ratio of sample size (e.g., number of cougar locations) to number of model parameters in the global model was less than 40 (Burnham and Anderson 2002). The number of estimable parameters (*K*) included only the slope parameters (β‘s) because the conditional logistic model does not have an intercept (Allison 1999). For categorical variables, the number of estimated parameters was for n-1 levels of the variable. I also calculated Akaike weights, which provide a means of evaluating the weight of evidence in favor of one model being the best given the set of candidate models (Burnham and Anderson 2002). Interpretation of coefficients in the "best" model was achieved by exponentiating the β's to obtain the odds ratios. A 95% confidence interval was constructed around each odds ratio to determine the significance of each variable.

Where the overall analysis of effects for a categorical variable was significant (i.e., 95% confidence interval around the odds ratio did not include 1) in the "best" model, I conducted contrast tests for post-hoc pair-wise comparisons of the different levels of the variable and to generate odds ratios. For example, if there were 5 levels to a categorical variable, there would be 10 pair-wise comparisons. To do this, I used the CONTRAST statement in PROC LOGISTIC. These contrast tests used effect coding to determine if the β's for each level were different from zero and enabled estimation of the odds ratio for every paired comparison (one level of the variable compared to another level). As a result of the effect coding, the parameter estimates represent the difference in the effect of each level of the categorical variable compared to the average effects of all levels. The computed statistic in the contrast tests is based on the Wald statistic. I

calculated 95% confidence intervals around the odds ratios. I also used FDR procedures to correct for the multiple comparisons conducted in the contrast tests.

Model Validation. – Methods used in assessing model performance with presence-absence data (e.g., receiver operating characteristic curves, Kappa) are not appropriate for use-availability studies because the data are not mutually exclusive (Boyce et al. 2002). I used the k-fold cross-validation method described by Boyce et al. (2002) for use-availability data, which I implemented using SAS. For each of the 6 selected "best" models, the data were divided into 5 equal subsets, accounting for the fact that each cougar had a different number of locations. The division into subsets also maintained the matching structure of the data. Models were constructed or trained using 4 of the 5 subsets (80% of the data) and validated with the last subset (20%). This was repeated 4 more times, such that each subset was used as the validation data once and was included in the training data 4 times.

For each of the 5 folds, I binned the predicted values for the validation data (i.e., the 20% subset of used locations) into 10 categories with an equal number of observations in each bin (Boyce et al. 2002). The bins were ordinal with the lower ranked bins indicating low relative probability of use and the higher ranked bins indicating high probability of use. For example, bin 1 represented predicted values that were approximately ≥ 0.00 and < 0.10, bin 2 represented values ≥ 0.10 and < 0.20, and so forth. To test model performance, I compared the frequencies of validation points within each bin (adjusted for area) and the bin rank. Boyce et al. (2002) stated that the area-adjusted frequency for each bin was the "frequency of cross-validated use locations

within a bin adjusted (divided) by the area of that range of values available" in the study area. The area-adjusted frequency (*f*) would be calculated as:

$$f = \frac{u_i}{a_i} * 0.1,$$

where u_i is the proportion of use (validation) observations within bin *i*, and a_i is the proportion of available study pixels in bin *i*. Because 10 bins were used, a proportion of 0.1 was used to standardize the available pixels in each bin (scales to 1).

Because I did not have spatial data representing the model output values as pixels, I could not calculate the area adjustment in sensu Boyce et al. (2002). Instead, for each bin I calculated a ratio of the proportion of used locations to the proportion of available (used + random) locations. This is a sampling method rather than a census method for estimating the area of predicted values across the study site. The model attempts to distinguish used locations from available locations. If the model is ineffective, the ratio would be 1 for every bin, indicating validation (use) locations occurred at rates expected by chance. The "area" adjustment corrects for the potential of having fewer observations in certain bins because those values were rare in the study area even though there could be more observations per unit area.

I calculated a Spearman-rank correlation between the "area"-adjusted frequency in each bin and the bin number. A good predictive model was one that showed a significant, positive rank correlation, indicating it predicted validation data (use locations) well. That is, a good model would have more use locations falling in higher ranked bins that represent higher predicted probabilities of use.

RESULTS

Telemetry

Over 11 field seasons, 76 adult and sub-adult cougars were radio-collared on the Monroe site (31 males, 45 females). Over 10 field seasons on the Oquirrhs site, 39 cougars (14 males, 25 females) were collared. Excluding GPS collar data, approximately 94% of radiolocations from the Oquirrhs and 86% of radiolocations from Monroe were collected via daytime aerial telemetry. The remainder were collected using ground-based telemetry or by recording the coordinates of a track or visible cougar with a handheld GPS unit. The sex ratios on both study sites were biased towards females. Females were also monitored 2 to 4 times longer than males because males tended to emigrate from the study sites and had shorter life spans than females (Wolfe et al. 2004).

From 2002-2007, GPS collars were placed on 15 resident adult cougars on the Oquirrh Mountains. One of these cougars left the study site, and 2 died after wearing GPS collars for only a few days. GPS data used in the home range and habitat analyses conducted in this study were from the remaining 9 female and 3 male cougars (Table 2). These cougars wore GPS collars over a 3- to 36-month period beginning in the winter field season. Of the approximately 18,000 GPS collar locations acquired, 61% were collected during nocturnal hours, 23% during crepuscular hours, and 16% during diurnal hours.

Table 2. Data from GPS collars worn by 3 male and 9 female cougars on the Oquirrh Mountains, Utah, USA, 2002-2007, separated by year when cougars wore different collars over multiple years.

Animal ID (year)	No. daily locations scheduled	No. locations acquired	% successful fixes	% 3D	Mean DOP
F06	6	1858	85.2	61.5	3.3
F12 (y1)	7	441	76.9	53.1	2.9
F12 (y2) [a]	7	828			
F18 (y1)	7	1646	74.8	51.4	3.3
F18 (y2)	8	2305	85.1	62.7	2.9
F18 (y3)	5	728	37.2	40.0	3.1
F19 (y1)	7	1308	65.8	41.4	3.3
F19 (y2)	5	640	32.4	41.1	3.1
F20	5	806	53.4	43.4	3.0
F26	8	1491	54.6	47.8	3.4
F37	7[b]	460	27.9	31.5	3.2
F58 (y1)	8	1893	72.5	43.9	3.5
F58 (y2)	8	1330	49.9	37.8	3.4
F68	7	535	67.3	61.7	3.1
M15a	8 [c]	888	74.1	78.6	4.9
M16	5	227	35.6	30.4	2.8
M33	7 [d]	674	33.0	29.4	3.3
Mean			61.8	49.6	3.3

[a] not included in statistical analysis of fix rate because data were acquired after the analysis was completed.
[b] in addition, 1 day per week the collar attempted a fix every hour.
[c] in addition, 1 day per week the collar attempted a fix every 30 minutes
[d] 1 day per week the collar attempted 15 fixes within 24 hours
skewed (skewness statistic = 2.42). Removing 3 very large errors (> 2,000 m) reduced

Telemetry Accuracy

The aerial telemetry location error averaged 628 m (n = 34, SD 760 m). The median error (380 m) was less than the mean error, making the distribution positively the mean error to 459 m. Because the error data were positively skewed, I averaged the mean and median errors to find an appropriate buffer size to use around aerial telemetry locations used in the resource selection analysis. This resulted in an error buffer of 500 m.

Data used to test the accuracy of the GPS collars were from 5 collars (4 cougar mortalities, 1 test collar), which were stationary for at least 3 weeks (Table 3). The errors ranged from 1 m to 316 m, and the mean error for all stationary data (pooled) was 14.6 m (n = 815, SD 24.0). The accuracy of a location varied by the DOP and whether it was a 2D or a 3D fix (Figure 5). Twelve locations (1.5%) had errors of 100 m or greater. Four locations (0.5%) had errors of 150 m or greater, all of which were 2D locations. Some locations exhibited high DOP but low error (and vice versa). The 2D locations were less accurate and less precise overall than 3D locations, as evident by the larger mean error (18.1 vs. 9.1) and standard deviation (28.9 vs. 10.51). Fix rates varied collar-to-collar for these stationary tests, but did not vary by time of day (i.e., crepuscular, diurnal, nocturnal).

GPS Collar Fix Rate

Average fix rate for GPS collars worn by live cougars was comparable to the average fix rate for the stationary collars but the rate varied by individual (range 28 –

Table 3. Data from stationary GPS collars used to estimate fix rate and location error for data used in the cougar habitat study on the Oquirrh Mountains, Utah, 2002-2007.

Test	No. locations	No. days	Mean error (m)	% successful fixes
Test collar	177	14	8.4	74.5
M14 mortality	73	20	6.8	53.4
M15a mortality	311	32	20.3	74.5
F08 mortality	185	43	16.0	62.4
F37 mortality	69	45	10.3	18.7
Mean (pooled data)			14.6	56.7

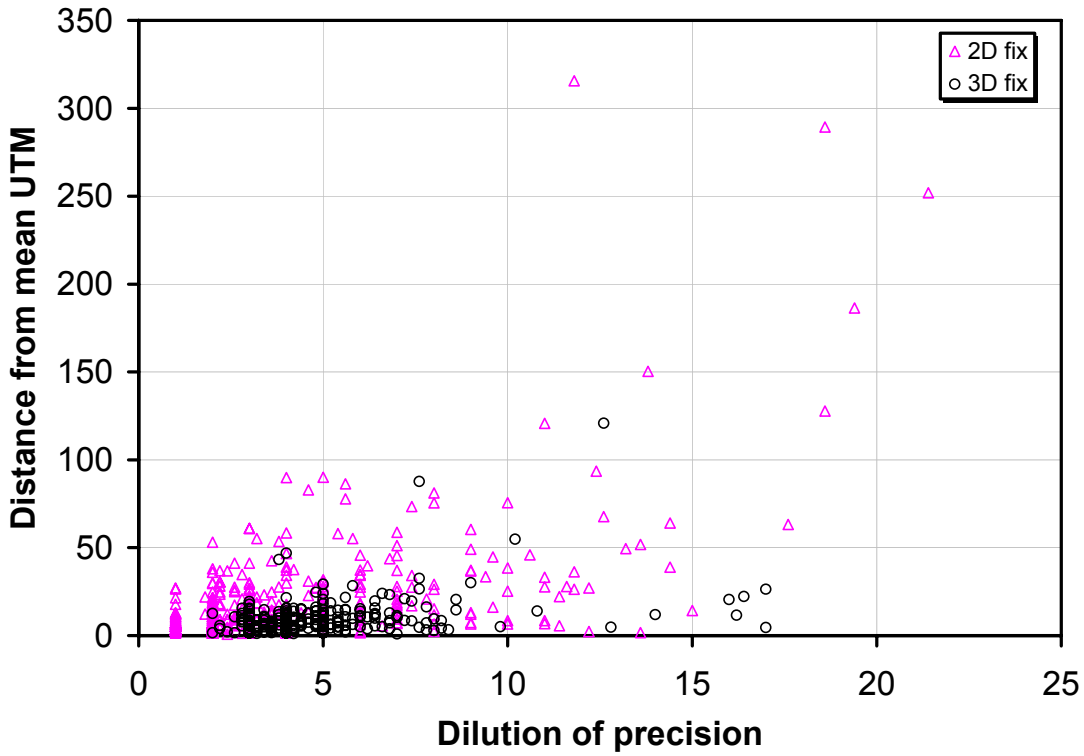

Figure 5. Scatterplot to evaluate the influence of dilution of precision and presence of elevation value (2D vs. 3D fix) on the accuracy of coordinates acquired with the GPS collars. Data were 815 locations from 5 stationary GPS collars.

85%) (Table 2). Fix rates for collars programmed for 5 locations per day (2005-2006 season) were particularly low across all cougars (less than 50% in most cases). Fix rate varied each year for individuals that were monitored over multiple years. There appeared to be a positive relationship between collar fix rate and proportion of 3D locations acquired by a collar worn by live cougars. Forty-seven percent of locations were 3D.

In contrast with the stationary collars, fix rates for collars worn by live cougars varied by time of day (Table 4). Fix rates were lowest during diurnal hours and greatest during crepuscular and nocturnal hours (Figure 6). Cell chi-square values indicated that most of the variation in fix rates by time of day was due to fewer than expected fixes diurnally. The results of the Mantel-Haenszel test for average effects across all cougars indicated that fix rate was associated with time of day after controlling for differences among cougar ($MH = 472.45$, $df = 2$, $p < 0.001$).

Table 4. Results of chi-square tests for homogeneity of GPS collar fix rates across 3 times of day for 12 cougars on the Oquirrh Mountains, Utah, 2002-2007. All degrees of freedom = 2.

Cougar	Pearson chi-square	P-value
F06	10.67	0.005
F12	15.18	0.001
F18	204.77	< 0.001
F19	160.67	< 0.001
F20	92.26	< 0.001
F26	60.50	< 0.001
F37	7.17	0.028
F58	29.17	< 0.001
F68	1.26	0.533
M15a	9.15	0.010
M16	27.96	< 0.001
M33	8.15	0.017

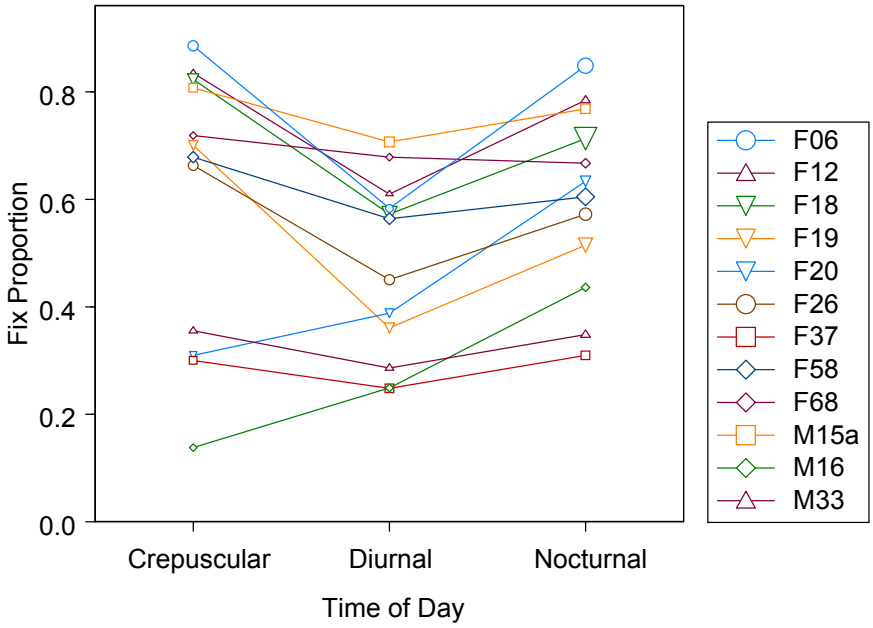

Figure 6. GPS collar fix rate by time of day for 12 cougars on the Oquirrh Mountains, Utah, 2002-2006. Symbol size is proportional to number of fix events in each category relative to the number of fix events for the whole study (not within animal).

Fix rate proportions varied among the 4 seasons (Table 5). Successful fixes occurred in greatest proportion in spring and summer months, and lowest proportion in winter and fall, with a pronounced peak success in spring (Figure 7). Cell chi-squared values indicated that the difference in seasonal fix rates was primarily due to more fixes than expected in spring. The results of the Mantel-Haenszel test for average effects across all cougars indicated that fix rate was associated with season after adjusting for individual cougar ($MH = 511.58$, $df = 3$, $p < 0.001$).

Table 5. Results of chi-squared tests for homogeneity of proportions for GPS collar fix rate over 4 seasons for 7 cougars on the Oquirrh Mountains, Utah, 2002-2006. All degrees of freedom = 3.

Cougar	Pearson chi-square	P-value
F06	5.84	0.12
F18	127.67	< 0.0001
F19	284.94	< 0.0001
F20	8.66	0.03
F26	130.92	< 0.0001
F58	221.24	< 0.0001
M33	29.71	< 0.0001

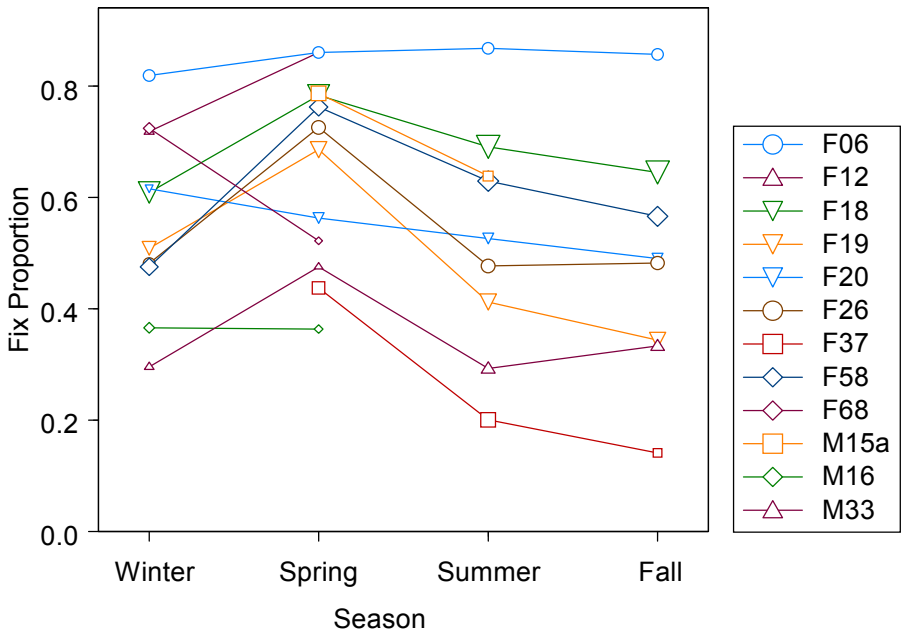

Figure 7. GPS collar fix rate by season for 12 cougars on the Oquirrh Mountains, Utah, 2002-2006. Symbol size is proportional to number of fix events in each category relative to the number of fix events for the whole study (not within animal).

In the 2-season analysis, 60% of cougars had a greater proportion of successful fixes than expected in spring than in winter (Table 6). For these cougars, the odds of a fix in spring months were 2 to 3 times the odds of a fix in winter months. The Breslow-Day test indicated that the proportions were not homogenous across all cougars for the 2 seasons (Chi-square = 187.68, df = 9, $p < 0.001$). Therefore, I did not calculate a MH statistic for the 2-season table.

Table 6. Results of chi-square tests for homogeneity of proportions for GPS collar fix rate across 2 seasons for 10 cougars on the Oquirrh Mountains, Utah, 2002-2006. Odds ratios give the odds of a successful fix in spring compared to winter. All degrees of freedom = 1.

Cougar	Pearson chi-square	P-value	Odds ratio (OR)	95% confidence interval on the OR
F06	3.37	0.07	1.361	0.9784 – 1.893
F12	15.10	0.0001	2.417	1.536 – 3.805
F18	115.84	< 0.0001	2.325	1.990 – 2.715
F19	58.70	< 0.0001	2.107	1.739 – 2.552
F20	1.14	0.29	0.805	0.541 – 1.200
F26	78.82	< 0.0001	2.847	2.253 – 3.598
F58	208.29	< 0.0001	3.539	2.971 – 4.216
F68	26.12	< 0.0001	0.416	0.296 – 0.586
M16	0.003	0.96	0.991	0.705 – 1.392
M33	18.82	< 0.0001	2.157	1.520 – 3.061

Home Range Estimation

Multi-year Diurnal Home Ranges from Aerial Telemetry

I estimated multi-year, diurnal home ranges for 17 cougars (3 males, 14 females) on the Oquirrhs site and 20 female cougars (no males) on the Monroe site. Because of

the short-lives of male cougars relative to the frequency of aerial telemetry flights, only the males who wore GPS collars on the Oquirrhs had sufficient locations to estimate a home range. On average, it took 42 locations on the Monroe site and 41 locations on the Oquirrhs site for home range area estimates to reach an asymptote. Linear regression indicated there was no relationship between number of locations and either fixed kernel (FK) or minimum convex polygon (MCP) home range area estimates (Table 7).

Table 7. Results of linear regression of number of radiolocations on home range size estimated using minimum convex polygon (MCP) and fixed kernel density (FK) algorithms.

Study site	Home range algorithm	R-squared	P-value
Oquirrhs (df = 16)	MCP	0.05	0.38
	FK	0.18	0.09
Monroe (df = 19)	MCP	0.03	0.48
	FK	0.00	0.85

Individual female FK home range estimates varied widely, ranging from 26 to 192 km^2 on the Oquirrhs (Table 8) and from 67 to 310 km^2 on Monroe (Table 9). Mean FK home range sizes for female cougars on Monroe were approximately 2 times the mean FK home range for females on the Oquirrhs, and the mean MCP estimate was 1.5 times larger on Monroe. Female home ranges on Monroe also exhibited greater variability in size compared to female home ranges on the Oquirrhs (SD on 95% FK = 76 km^2 and 42 km^2, respectively). On the Oquirrhs, the average male home range FK estimate was 60% larger than the average estimate for females on the site. Male home ranges on the Oquirrhs were similar in size to the female home ranges on Monroe. The average male home range estimate from the Oquirrhs was more representative of annual

Table 8. Multi-year diurnal home range estimates for 14 adult female and 3 adult male cougars in the Oquirrh Mountains, Utah, USA, 1997-2007, using minimum convex polygon (MCP) and fixed kernel (FK) estimators (from aerial, ground, and diurnal GPS collar telemetry).

Animal ID	No. years	Aerial telemetry data				Aerial telemetry + diurnal GPS collar data			
		No. locations	MCP area (km^2)	95 % FK area (km^2)	LSCV h-value (m)	No. locations	MCP area (km^2)	95 % FK area (km^2)	LSCV h-value (m)
F06	2	22	*i/d* [a]	*i/d*	*i/d*	280	66	52	490
F12	5	26	*i/d*	*i/d*	*i/d*	197	67	52	627
F13	4	63	173	74	976	*n/a* [b]	*n/a*	*n/a*	*n/a*
F18	3	44	65	41	779	451	70	26	472
F19	3	41	95	120	1409	198	107	84	969
F20	3	19	*i/d*	*i/d*	*i/d*	100	50 [c]	77	1247
F26	2	11	*i/d*	*i/d*	*i/d*	96	73 [c]	87	1352
F37	0.75	8	*i/d*	*i/d*	*i/d*	99	237	115	1704
F53	5	81	96 [c]	192	1745	*n/a*	*n/a*	*n/a*	*n/a*
F56	2	41	48	71	875	*n/a*	*n/a*	*n/a*	*n/a*
F58	7	106	69	76	703	315	75	60	542
F59	6	84	116	105	911	*n/a*	*n/a*	*n/a*	*n/a*
F62	3	60	61	47	671	*n/a*	*n/a*	*n/a*	*n/a*
F68	5	92	46	47	593	160	52	45	517
Female mean			85	86	962		92	78	936
M15a	1.5	27	*i/d*	*i/d*	*i/d*	79	99	130	1040
M16	3	29	200	298	1987	67	220	223	1526
M33	1	14	*i/d*	*i/d*	*i/d*	127	149	151	1288
Male mean							156	168	1285

[a] *i/d* = insufficient data to calculate a home range

[b] *n/a* = no GPS collar data available

[c] calculated by adding areas of disjunct home ranges

Table 9. Multi-year home range estimates for 20 adult female cougars on Monroe Mountain, Utah, USA, 1997-2006, using minimum convex polygon (MCP) and fixed kernel (FK) estimators (from diurnal aerial and ground telemetry).

Animal ID	No. locations	No. years	MCP area (km^2)	95% FK area (km^2)	LSCV h-value (m)
F01	43	2	301	218	1,764
F03	57	3	93	101	939
F04	43	2	147	191	1,474
F05	69	4	463	297	2,283
F06	40	2	109	116	1,174
F08	65	3.5	174	159	1,322
F09	32	1.5	59	86	1,021
F12	102	6	102	92	856
F16	50	3	226	213	1,521
F17	31	1.5	192	256	1,882
F26a	31	2	46	67	850
F30	31	3	117	181	1,891
F32b	47	5	80	107	972
F35	39	5	333	310	2,175
F36	44	5	107	103	1,095
F40	40	4.5	267	233	1,877
F43	38	4	65	76	940
F49	39	3.5	81	113	1,063
F52	30	3	221	190	1,882
F53	36	3	93	140	1,390
Female mean			164	163	1,419

than lifetime estimates because only 1 of the 3 males was monitored longer than 1.5 years.

Five female and 2 male cougars lacked sufficient aerial telemetry data to generate a home range but I was able to estimate their home ranges with the addition of the diurnal GPS collar data. There were 5 instances (i.e., F18, F19, F58, F68, and M16) where I estimated a cougar's home range from both the aerial telemetry data and the aerial

telemetry supplemented with the diurnal GPS data. In these cases, the estimated MCP area for a cougar's 2 home ranges were similar, differing by 7 km^2 or less for females and 20 km^2 for males (Table 8). However, the FK estimates differed substantially; in some cases the percent difference was as high as 32%.

Some cougars on the Oquirrh Mountains used disjunct winter and summer home ranges, which was apparent in the fixed kernel home range delineations. These cougars migrated each winter down to the lower elevations of the Traverse Range portion of the Oquirrhs complex, or in one case crossed the ridge of the Oquirrhs to use the foothills on the west-side. Migratory cougars on the Oquirrhs exhibited the largest home ranges whereas cougars inhabiting Camp Williams year-round exhibited the smallest home ranges. The size of the area used in any one season (winter or summer) by migratory cougars was comparable to the total area used annually by cougars that did not migrate. On the Monroe site, no female home ranges were disjunct due to seasonal migration, although cougars with spruce-fir and aspen forests occurring in their home range tended to shift activity to lower elevations in winter. The largest home ranges on Monroe Mountain were used by cougars in the southern portion of the study area and by cougars whose home range included adjacent mountain ranges.

On both study sites female home ranges overlapped extensively. Maps of cougar home ranges are presented in Appendix D for the Oquirrhs and Appendix E for Monroe. Females on the Oquirrhs often occupied nearly the same boundaries (e.g., Figure D.3 in Appendix D). The greatest overlap on the Oquirrhs occurred during winter of 2006 on Camp Williams, when up to 5 female cougars and at least 1 male cougar used the property during the same time period (Figure D.5 in Appendix D). On the Oquirrhs, male

home ranges overlapped multiple female home ranges (Figures D.4 and Figure D.5 in Appendix D). There was no overlap in home ranges for the 2 male cougars that were monitored over the same time period. The Bingham copper pit separated their ranges.

Cougar home ranges on both study sites were restricted to mountainous terrain. The main ridgeline of the mountains on both study sites often served as an approximate home range boundary for females. Home ranges included minor mining pits on the Oquirrhs, but no home range encompassed the main Bingham pit. The pit apparently served as a home range boundary for both males and females. Female FK home ranges usually excluded the impact area on Camp Williams, which is used intensively by the military for artillery and small arms live fire.

Annual Home Ranges from GPS Collar Data

Annual home ranges were estimated for 12 cougars on the Oquirrh Mountains using GPS collar locations acquired over all times of day (Table 10). For female cougars, the average annual MCP and FK home ranges estimated from GPS collar data differed by 14 km^2 from the average multi-year MCP and FK home ranges estimated using solely aerial telemetry data. The GPS home ranges estimated from all times of day were larger than aerial telemetry home ranges. While this seems counterintuitive because the GPS data encompassed only 1 year and the aerial telemetry data covered multiple years, the result is likely due to the GPS collar data having a larger sample size and coverage of times of day when cougars were most active.

Table 10. Home range estimates using GPS collar locations from all times of day for 9 adult female cougars and 3 adult male cougars in the Oquirrh Mountains, Utah, USA, 2002-2007. See Table 2 for sample sizes.

Animal ID	Year	No. months	% locations by diel category[a]	MCP (km^2)	95% FK (km^2)	H-value
F06	2002-2003	12	1% D, 18% C, 81% N	75	68	700
F12	2003	3	14% D, 21% C, 65% N	60	64	700
	2006-2007	12	26% D, 20% C, 54% N	87	64	600
F18	2003-2004	10	23% D, 13% C, 64% N	53	46	1,000
	2004-2005	11	33% D, 16% C, 51% N	64	57	1,000
	2005-2006	13	25% D, 2% C, 73% N	108	87	1,000
F19	2003	9	24% D, 17% C, 59% N	98	76	1,200
	2005	13	28% D, 4% C, 68% N	129	87	700
F20	2005	11	27% D, 1% C, 72% N	68	50	600
F26	2004	11	33% D, 16% C, 51% N	167[b]	88	1,300
F37	2006	6	41% D, 15% C, 44% N	220[b]	159	1,600
F58	2002-2003	11	14% D, 21% C, 65% N	53	42	600
	2003-2004	10	31% D, 14% C, 55% N	59	38	500
F68	2002-2003	4	14% D, 16% C, 70% N	38	36	400
Female mean[c]				99	72	867
M15a	2006	3	51% D, 15% C, 34% N	117	67	1,000
M16	2004-2005	4	25% D, 2% C, 73% N	289	219	1,500
M33	2006	8	27% D, 17% C, 56% N	198	144	1,000
Male mean				201	143	1,167

[a] D= diurnal, C = crepuscular, N = nocturnal

[b] Used disjunct seasonal home ranges. MCP was around all locations for the year.

[c] If there was more than 1 year of data on the same animal, I used a within animal mean for that individual when calculating the female mean

Nocturnal MCP home ranges were larger than diurnal MCP home ranges for all cougars but F37 (Table 11). Nocturnal FK home ranges were larger than diurnal FK home ranges for all cougars but M15a. Female MCP nocturnal home ranges were 15% larger on average than diurnal MCP home ranges, and FK ranges were 28% larger. Male MCP nocturnal home ranges were 21% larger on average and FK nocturnal ranges were 28% larger on average than male diurnal MCP and FK home ranges. Diurnal MCP and FK home ranges were usually nested within the nocturnal home range, and were similar in shape and outer boundaries. The majority of locations forming outer home range boundaries were nocturnal locations rather than diurnal locations.

Home ranges were similar in size for all seasons. There was no pattern indicating smaller or larger home ranges in any given season. Monthly home ranges averaged 33 km^2 for female cougars and 113 km^2 for males. On average, female cougars used 37% of their total annual home range over a month, and male cougars used 53% of their total GPS home range (estimated from a 3-8 month period) over a month.

Delineating monthly home ranges revealed female natal denning events. Natal denning was documented in 5 female cougars by a decrease in monthly home range size in conjunction with repeated use of the same vegetation patch for at least 4 weeks. The majority of natal denning was confirmed by aging of kittens in the field. Over the 3 months following den initiation, a mother cougar's average quarterly home range size was 10 km^2, a two-thirds reduction in size compared to prior quarters (Figure 8). Even 3 to 6 months after denning, quarterly home ranges were half the size of the quarterly ranges used prior to denning.

Table 11. Nocturnal and diurnal home range sizes estimated from GPS collar data for 9 female and 2 male cougars on the Oquirrh Mountains, Utah.

Cougar ID	Diurnal			Nocturnal		
	No. locations	MCP (km^2)	95% FK (km^2)	No. locations	MCP (km^2)	95% FK (km^2)
F06	9	*i/d*[a]	*i/d*[a]	1,849	75	68
F12-year 1	50	28	32	391	58	66
F12-year 2	219	62	42	609	82	71
F18-year 1	351	41	40	1,299	51	46
F18-year 2	693	44	47	1,617	63	58
F18-year 3	181	70	55	549	108	92
F19-year 1	258	79	54	1,050	94	83
F19-year 2	181	101	105	459	124	130
F20	216	48	40	589	65	52
F26	406	136	80	1,085	167	91
F37	190	218	110	268	212	181
F58-year1	256	41	35	1,637	52	43
F58-year2	411	47	40	919	58	37
F68	77	27	27	458	38	35
Female mean[b]		82	57		96	79
M15a	610	100	86	588	109	69
M16	58	193	148	169	259	247
M33	183	154	133	491	198	154
Male mean		149	122		189	157

[a] *i/d* = insufficient data available to estimate a home range

[b] If there was more than 1 year of data on the same animal, I used a within animal mean for that individual when calculating the female mean

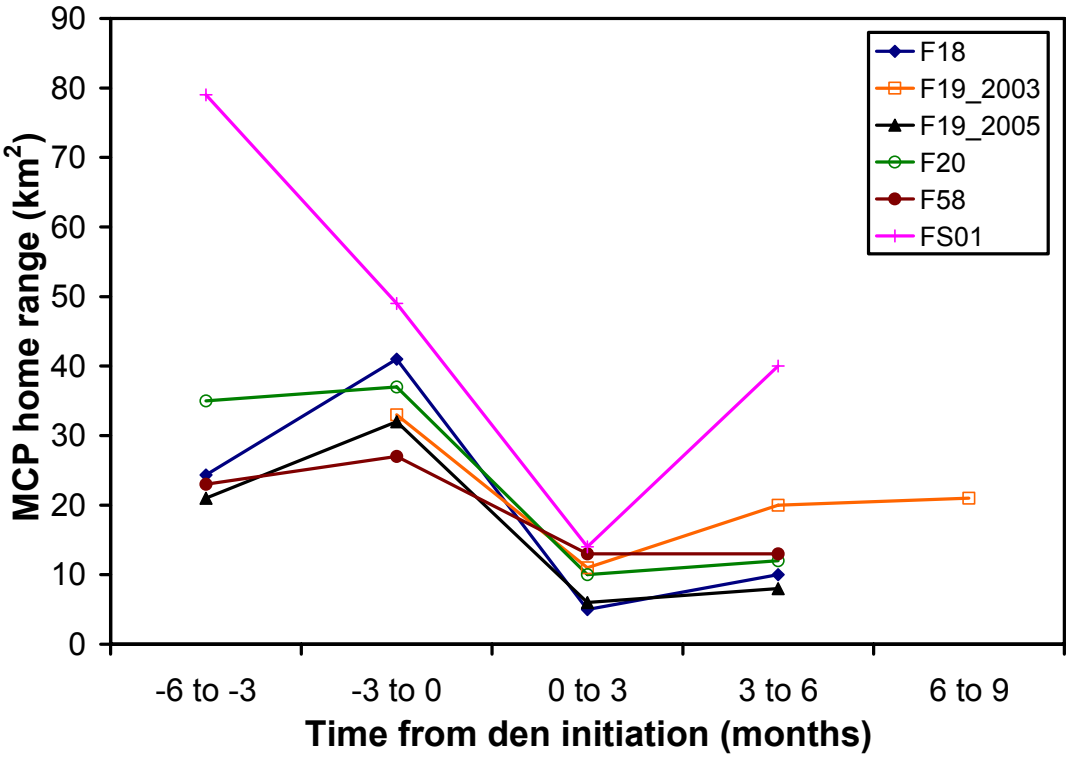

Figure 8. Quarterly minimum convex polygon (MCP) home range estimates using GPS collar data from years when natal denning occurred on the Oquirrh Mountains, Utah, 2002-2005. Monthly home ranges were averaged to get the quarterly estimates.

Females usually used a primary natal den, where parturition likely occurred, for approximately 1 month. After that period, mothers moved kittens 1 to 3 times to auxiliary dens, which were used for 1 to 4 weeks. Auxiliary dens were located 225 m to 2,500 m from the primary natal den. F19 bore litters in 2 different years, but she used different dens each year. All births occurred in warmer months from May to September (Table 12).

Table 12. Number of litters born by month as determined with GPS collar data from 5 female cougars on the Oquirrh Mountains and Stansbury Mountains, Utah, 2002-2007.

Month	Number of litters	Cougar
January		
February		
March		
April		
May	1	F19
June	1	F20
July	2	F58, FS01[a]
August	1	F19
September	1	F18
October		
November		
December		

[a] inhabited adjacent mountain range (Stansbury Mountains)

Resource Selection

Coarse Level: Diurnal Use Versus Availability

Land Cover. – The 2 study sites differed in their proportional availability of land cover types as quantified by the random home range simulations. Furthermore, the proportionality of land cover across the 1,000 random home ranges differed from the overall distribution of land cover across the study areas, particularly for the most common cover types. That is, home range sized areas had different vegetation composition compared to the study areas as a whole. This was true when comparing average proportions, and when examining the distribution of proportions of cover types across the entire set of random home ranges. For example, on the Oquirrhs, the proportion of deciduous woodland in the study area was 0.197 but the mean proportion in the female-sized random home ranges was 0.301, a difference of more than 10%. The

results from this study confirm that spatial pattern affects estimates of availability and that land cover types were clumped rather than uniformly distributed across the study areas. Habitat proportions in a random home range would equal overall proportions in the study area only when habitat types are evenly distributed and occur in patches smaller than the home range size (Wilson et al. 1998). For example, if 4 vegetation types were equally abundant and aggregated on the study site, the proportions in a home range-sized area would equal the overall proportions in the study site only if the home range was centered where the 4 types were adjoining (Katnik and Weilgus 2005). Using spatially-explicit estimates of availability also allows modeling across the full range of vegetation composition that may occur in a home range.

Compared to Monroe Mountain, random female-sized home ranges on the Oquirrh Mountains contained greater proportions of deciduous woodlands and disturbed types on average, and smaller proportions of coniferous and deciduous forests, coniferous woodlands, and shrublands (Figure 9). The most common land cover type on the Oquirrhs site was deciduous woodland, which composed 30% of a random home range on average. On the Monroe site coniferous woodlands were the dominant type (26% composition).

A Kolmogorov-Smirnov test was used for each cover type to determine whether the distribution of proportions of a cover type for cougar home ranges differed from the distribution of that cover type for random home ranges. At the second-order level of resource selection (home range within a study area), I did not detect selection by cougars for specific land cover types on the Oquirrhs site after using the Bonferroni correction to adjust p-values to be more conservative. The Bonferonni correction was used to reduce

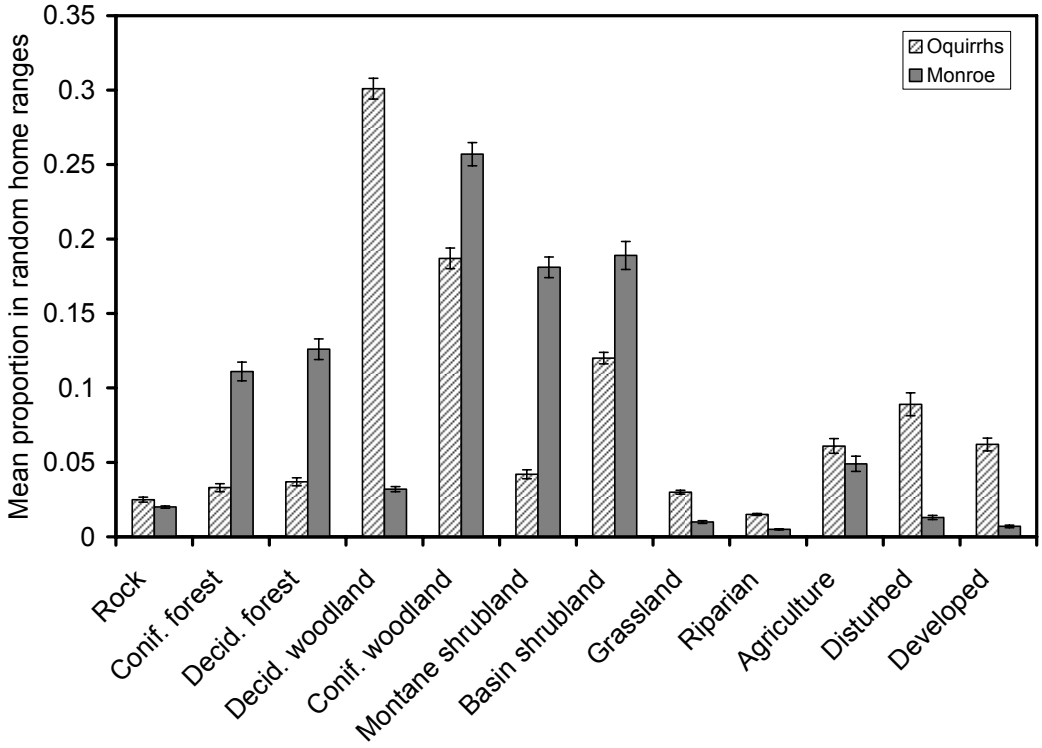

Figure 9. Comparison of proportional availability of land cover types on the Oquirrh Mountains and Monroe Mountain cougar study sites in Utah. Mean proportions were quantified by 1,000 simulated random home ranges, which were the size of the average female home range on each study site. Error bars represent 95% confidence intervals.

the potential for Type I error that could result from testing a set of related hypotheses simultaneously (e.g., in this study, each land cover type was tested individually). However, in some cases land cover proportions in cougar home ranges were statistically different from proportions in random home ranges prior to the Bonferroni correction (Table 13).

Graphs of cumulative distributions were generated by first ordering the proportions of each cover type within cougar home ranges and within the 1,000 random home ranges in ascending order and then calculating the "step" for each data point to

Table 13. Proportions of land cover types in 95% fixed kernel home ranges of 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Rock	Conif. forest	Decid. forest	Decid. woodl.	Conif. woodl.	Mont. shrubl.	Basin shrubl.	Grass	Ripar.	Agric.	Dist.	Devel.
Females												
F06	0.038	0.030	0.059	0.314	0.143	0.024	0.129	0.032	0.016	0.019	0.126	0.069
F12	0.003	0	0	0.506	0.242	0.010	0.135	0.041	0.030	0.006	0.008	0.019
F13	0.042	0.072	0.068	0.427	0.165	0.149	0.062	0.010	0.003	0.003	0.001	0
F18	0.005	0.001	0	0.609	0.256	0.016	0.079	0.027	0.006	0	0.001	0
F19	0.011	0.004	0.018	0.381	0.303	0.076	0.142	0.026	0.005	0.002	0.016	0.017
F20	0.041	0.072	0.066	0.462	0.068	0.061	0.112	0.065	0.018	0	0.015	0.021
F26	0.036	0.039	0.063	0.381	0.178	0.080	0.094	0.021	0.007	0	0.101	0.001
F53	0.032	0.073	0.067	0.230	0.175	0.111	0.127	0.030	0.020	0.037	0.015	0.014
F56	0.047	0.043	0.059	0.274	0.119	0.020	0.125	0.021	0.015	0	0.220	0.059
F58	0.020	0.054	0.051	0.596	0.046	0.033	0.105	0.050	0.020	0	0.009	0.016
F59	0.038	0.065	0.063	0.376	0.098	0.042	0.122	0.059	0.023	0	0.014	0.101
F62	0.008	0.015	0.010	0.529	0.074	0.022	0.163	0.070	0.028	0.002	0.032	0.047
F68	0.027	0.027	0.041	0.363	0.136	0.023	0.106	0.026	0.019	0.005	0.151	0.078
Cougar mean	0.027	0.038	0.043	0.424	0.154	0.051	0.116	0.037	0.016	0.006	0.055	0.034
Cougar SD	0.016	0.028	0.027	0.109	0.077	0.042	0.027	0.019	0.009	0.011	0.071	0.033
Random mean	0.025	0.033	0.037	0.301	0.187	0.042	0.120	0.030	0.015	0.061	0.089	0.062
Random SD	0.028	0.043	0.044	0.112	0.111	0.048	0.063	0.021	0.011	0.080	0.125	0.068
$D_{n=13}$	0.388	0.309	0.324	0.421	0.222	0.347	0.304	0.304	0.306	0.467	0.274	0.313
P-value	0.042	0.172	0.134	0.021	0.551	0.091	0.186	0.186	0.180	0.007	0.289	0.161
Adjusted p-value	0.168	0.223	0.223	0.126	0.551	0.223	0.223	0.223	0.223	0.089	0.315	0.223

Table 13 (continued). Proportions of land cover types in 95% fixed kernel home ranges of 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Rock	Conif. forest	Decid. forest	Decid. woodl.	Conif. woodl.	Mont. shrubl.	Basin shrubl.	Grass	Ripar.	Agric.	Dist.	Devel.
Males												
M15a	0.050	0.072	0.073	0.425	0.075	0.044	0.105	0.036	0.024	0	0.063	0.033
M16	0.025	0.045	0.039	0.341	0.280	0.062	0.114	0.025	0.011	0.005	0.042	0.012
M33	0.021	0.034	0.050	0.403	0.245	0.073	0.080	0.014	0.008	0.010	0.062	0.001
Cougar mean	0.032	0.050	0.054	0.390	0.120	0.06	0.100	0.025	0.014	0.005	0.056	0.015
Cougar SD	0.016	0.020	0.017	0.044	0.110	0.015	0.018	0.011	0.009	0.005	0.012	0.016
Random mean	0.028	0.038	0.043	0.254	0.177	0.042	0.116	0.028	0.013	0.097	0.089	0.076
Random SD	0.017	0.025	0.024	0.051	0.079	0.026	0.037	0.014	0.007	0.055	0.064	0.047

determine the cumulative frequency. Each step was 1/number of cougars for the cougar home ranges and 1/1,000 for the random home ranges. These figures indicate that cougar use of deciduous woodlands was highly consistent because all male and female home ranges on the Oquirrhs included a greater proportion of this type than random home ranges (Figure 10). Cougar home ranges included 12% more of this type on average compared to its availability on the study site. Cougars also tended to select the rock/cliff/canyon type and avoid agriculture at the second order, though again the Bonferroni correction reduced the power to detect this difference.

Female cougars on Monroe Mountain used specific land cover types at the second order of selection (Table 14). In particular, they used a significantly greater proportion of coniferous woodlands compared to availability of this type on the study site when selecting a home range (Figure 11). They avoided basin shrublands, agriculture, and developed cover types at the second order.

For the third-order analysis, some cougars did not have all 5 land cover types in their home range (e.g., those with home ranges located at a lower elevation had no forest types). This resulted in structural zeroes in the tables. Because I conducted separate tests on each cougar, these types were dropped on an individual basis as needed and the degrees of freedom adjusted accordingly (Agresti 1996, Manly et al. 2002).

Results from the third-order analyses indicate that cougars on the Oquirrh Mountains used land cover types selectively, both on an individual basis and when considering the population (Table 15). Of 9 cougars that were selective, 8 used particular land cover types more or less than expected (Table 16). Specifically, all 8 cougars selected deciduous woodlands, and approximately half avoided shrublands when using

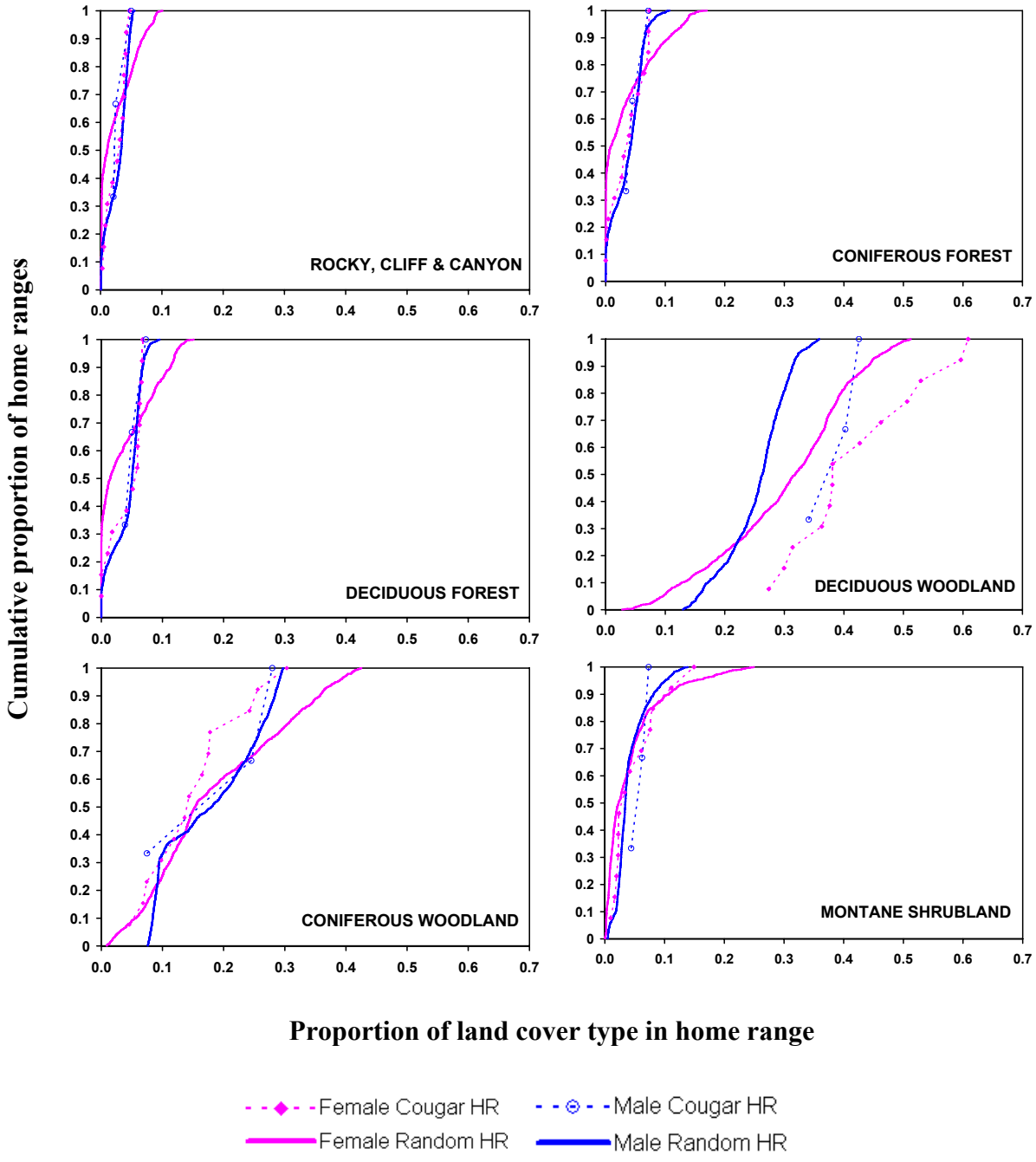

Figure 10. Cumulative distribution functions for proportion of land cover types in 13 female and 3 male cougar home ranges compared to proportion in 1,000 randomly placed home ranges on the Oquirrh Mountains, Utah. The random home ranges were circles with area equal to the mean cougar home range size for each sex on the study site.

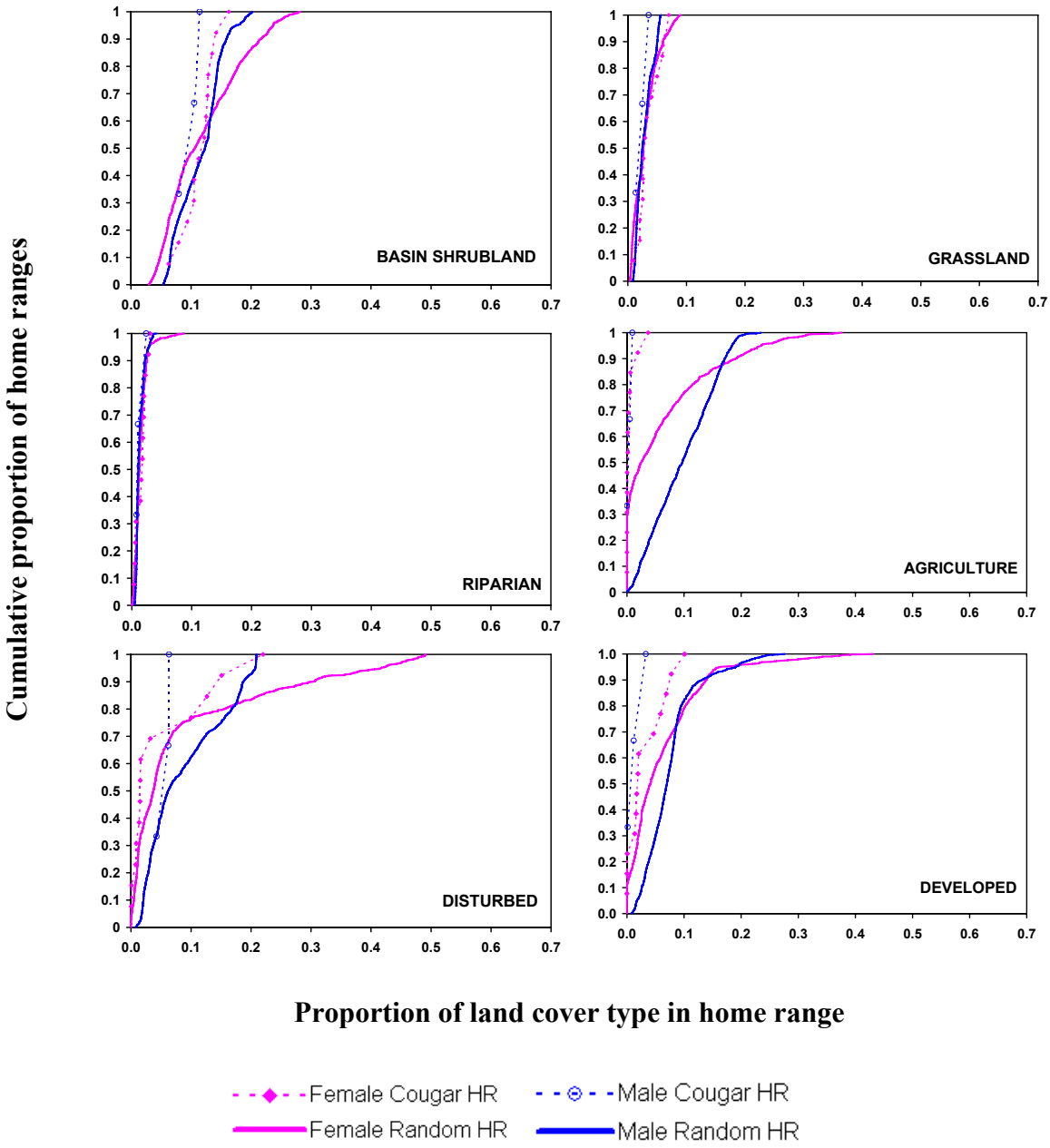

Figure 10 (continued). Cumulative distribution functions for proportion of land cover types in 13 female and 3 male cougar home ranges compared to proportion in 1,000 randomly placed home ranges on the Oquirrh Mountains, Utah. The random home ranges were circles with area equal to the mean cougar home range size for each sex on the study site.

Table 14. Proportions of land cover types in 95% fixed kernel home ranges of 20 female cougars on Monroe Mountain, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Rock	Conif. forest	Decid. forest	Decid. woodl.	Conif. woodl.	Mont. shrubl.	Basin shrubl.	Grass	Ripar.	Agric.	Dist.	Devel.
F01	0.006	0.118	0.222	0.085	0.203	0.319	0.040	0.004	0.005	0	0	0
F03	0.005	0.172	0.263	0.052	0.188	0.290	0.023	0.005	0.002	0.001	0	0
F04	0.006	0.161	0.275	0.014	0.152	0.306	0.059	0.006	0.001	0.017	0.004	0.001
F05	0.029	0.043	0.051	0.021	0.399	0.264	0.187	0.003	0.002	0.001	0	0
F06	0.009	0.084	0.184	0.018	0.257	0.360	0.069	0.003	0.003	0.008	0.003	0.001
F08	0.035	0.137	0.098	0.021	0.344	0.289	0.046	0.004	0.003	0.010	0.015	0
F09	0.036	0.199	0.160	0.074	0.403	0.075	0.039	0.008	0.007	0	0	0
F12	0.018	0.239	0.225	0.099	0.294	0.106	0.008	0.003	0.008	0	0	0
F16	0.041	0.183	0.164	0.037	0.237	0.210	0.089	0.003	0.002	0	0.034	0
F17	0.026	0.059	0.069	0.015	0.348	0.287	0.175	0.004	0.002	0.008	0.008	0
F26a	0.046	0.217	0.190	0.037	0.177	0.247	0.064	0.002	0.001	0	0.019	0
F30	0.058	0.091	0.064	0.065	0.407	0.089	0.199	0.012	0.009	0	0.005	0
F32b	0.013	0	0.001	0.082	0.668	0.093	0.126	0	0.019	0	0	0
F35	0.023	0.069	0.084	0.014	0.350	0.316	0.128	0.003	0.001	0	0.011	0
F36	0.020	0.015	0.074	0.012	0.525	0.230	0.115	0.004	0.002	0.004	0	0
F40	0.008	0.091	0.177	0.051	0.232	0.316	0.103	0.004	0.002	0.007	0.009	0.001
F43	0.062	0.106	0.089	0.041	0.375	0.173	0.128	0.001	0.002	0	0.024	0
F49	0.043	0.136	0.076	0.026	0.331	0.343	0.022	0.004	0.001	0	0.017	0
F52	0.043	0.079	0.050	0.017	0.391	0.069	0.296	0.004	0.009	0.008	0.033	0
F53	0.011	0.020	0.078	0.023	0.388	0.365	0.08	0.002	0.004	0.012	0.015	0.001
Cougar mean	0.027	0.111	0.130	0.040	0.333	0.237	0.100	0.004	0.004	0.004	0.010	0
Cougar SD	0.018	0.069	0.079	0.027	0.125	0.101	0.072	0.003	0.004	0.005	0.011	0.001

Table 14 (continued). Proportions of land cover types in 95% fixed kernel home ranges of 20 female cougars on Monroe Mountain, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

	Rock	Conif. forest	Decid. forest	Decid. woodl.	Conif. woodl.	Mont. shrubl.	Basin shrubl.	Grass	Ripar.	Agric.	Dist.	Devel.
Random mean	0.020	0.111	0.126	0.032	0.257	0.181	0.189	0.010	0.005	0.049	0.013	0.007
Random SD	0.012	0.102	0.112	0.027	0.126	0.111	0.152	0.014	0.006	0.083	0.021	0.014
$D_{n=20}$	0.275	0.236	0.283	0.218	0.411	0.275	0.413	0.296	0.174	0.439	0.162	0.380
P-value	0.103	0.225	0.087	0.309	0.003	0.103	0.003	0.064	0.593	0.001	0.682	0.007
Adjusted p-value	0.155	0.300	0.155	0.371	0.011	0.155	0.011	0.155	0.647	0.011	0.682	0.021

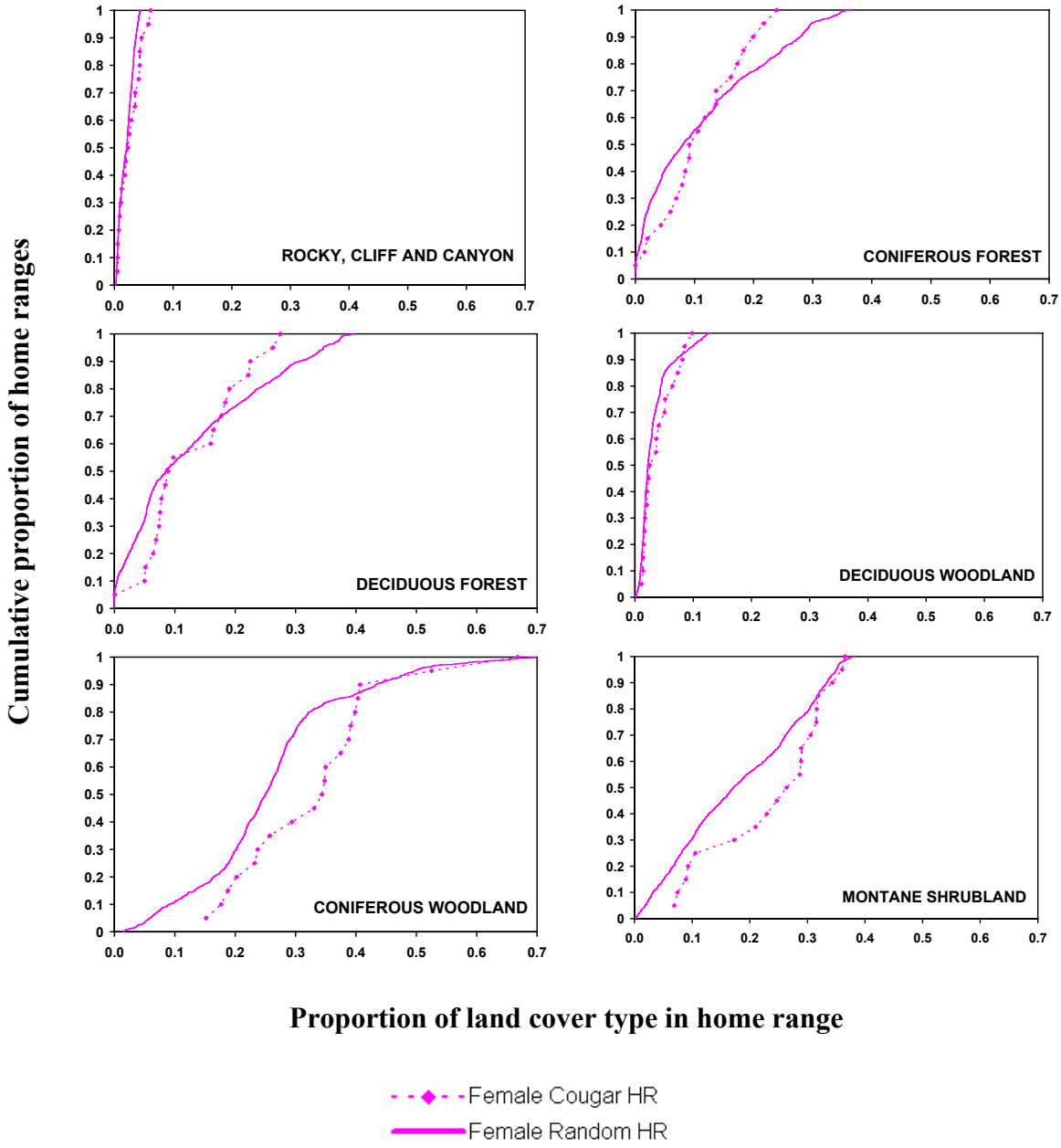

Figure 11. Cumulative distribution functions for proportion of land cover types in 20 female cougar home ranges compared to proportion in 1,000 randomly placed home ranges on Monroe Mountain, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

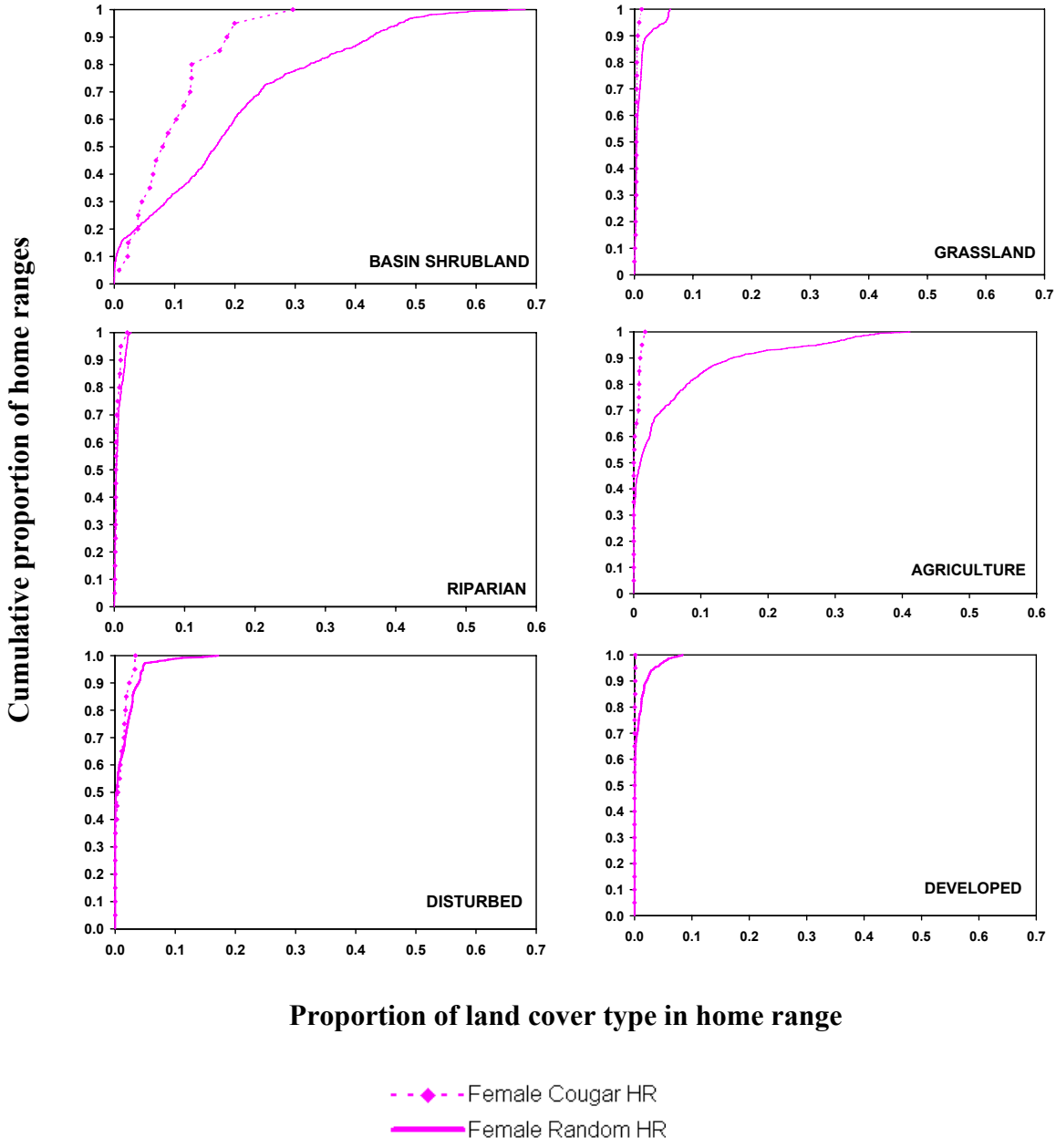

Figure 11 (continued). Cumulative distribution functions for proportion of land cover types in 20 female cougar home ranges compared to proportion in 1,000 randomly placed home ranges on Monroe Mountain, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

Table 15. Number of radiolocations observed (obs) and number expected (exp) in 5 land cover types for 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Third-order selection was tested at the individual level using chi-square goodness-of-fit tests (exact test used when expected counts were ≤ 5). An overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Conif. forest		Decid. forest		Decid. woodl		Conif. woodl.		Shrubland		X^2 statistic	df	P-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp			
F06	3	8	14	16	107	86	35	46	32	35	11.39	4	0.023
F12	NIHR[c]	NIHR	NIHR	NIHR	129	99	31	47	14	28	21.54	2	<0.001
F13	3	5	2	4	32	28	13	11	12	14	3.02	4	0.552[d]
F18	0	1	NIHR	NIHR	304	263	90	110	21	41	20.78	3	<0.001[d]
F19	2	1	2	3	96	74	52	59	28	43	13.94	4	0.012[d]
F20	4	8	3	7	74	50	2	7	8	19	25.75	4	<0.001[d]
F26	7	4	12	6	35	36	10	17	15	16	11.22	4	0.025[d]
F53	6	6	6	6	32	26	12	15	18	21	2.41	4	0.660
F56	1	2	3	3	18	14	4	6	6	7	2.45	4	0.663[d]
F58	12	17	15	16	211	184	10	14	25	42	13.52	4	0.009
F59	5	6	7	5	42	34	5	9	10	15	6.29	4	0.175[d]
F62	1	1	0	1	36	32	3	4	9	11	2.11	4	0.715[d]
F68	2	5	10	7	70	64	24	24	17	23	5.21	4	0.262[d]
M15a	4	6	5	7	54	38	3	7	5	13	15.18	4	0.005[d]
M16	2	3	2	3	30	23	19	19	7	12	4.88	4	0.293[d]
M33	2	4	8	6	72	51	23	31	6	19	21.27	4	<0.001[d]
Population											180.98	61	<0.001

[a] Obs = observed

[b] Exp = expected

[c] NIHR = "not in home range"; the vegetation type did not occur in the cougar's home range and therefore was not available for third-order selection.

[d] Exact p-value

Table 16. Selection ratios and their Bonferroni confidence intervals for land cover types used by 11 cougars on the Oquirrh Mountains, Utah, calculated only for cougars that demonstrated third-order selection in prior tests. Cougar use of a land cover type was significantly different from availability if the confidence interval did not include the value 1.

Cougar	Land cover type	Observed proportion	Expected proportion	Selection ratio	Standardized selection ratio	95% Bonferroni confidence interval
F06	Coniferous forest	0.016	0.042	0.375	0.090	0.000 [a] - 1.266
	Deciduous forest	0.073	0.084	0.875	0.210	0.259 - 1.491
	Deciduous woodland	0.560	0.450	1.244	0.298	1.038 - 1.450
	Coniferous woodland	0.183	0.241	0.761	0.182	0.430 - 1.092
	Shrubland	0.168	0.183	0.914	0.219	0.521 - 1.308
F12	Coniferous forest	NIHR [b]				
	Deciduous forest	NIHR				
	Deciduous woodland	0.741	0.569	1.303	0.529	1.133 - 1.473
	Coniferous woodland	0.178	0.270	0.660	0.268	0.339 - 0.981
	Shrubland	0.08	0.161	0.500	0.203	0.054 - 0.946
F18	Coniferous forest	0	0.002	0	0	0.000 [a] - 2.573
	Deciduous forest	NIHR				
	Deciduous woodland	0.733	0.634	1.156	0.465	1.060 - 1.252
	Coniferous woodland	0.217	0.265	0.818	0.329	0.608 - 1.029
	Shrubland	0.051	0.099	0.512	0.206	0.130 - 0.894
F19	Coniferous forest	0.011	0.006	2.000	0.364	0.000 [a] - 4.569
	Deciduous forest	0.011	0.017	0.667	0.121	0.000 [a] - 2.141
	Deciduous woodland	0.533	0.411	1.297	0.236	1.068 - 1.527
	Coniferous woodland	0.289	0.328	0.881	0.160	0.606 - 1.156
	Shrubland	0.156	0.239	0.651	0.118	0.308 - 0.994

[a] Negative lower limit was changed to 0.000.

[b] Not In Home Range

Table 16 (continued). Selection ratios and their Bonferroni confidence intervals for land cover types used by 11 cougars on the Oquirrh Mountains, Utah, calculated for cougars that demonstrated third-order selection in prior tests.

Cougar	Land cover type	Observed proportion	Expected proportion	Selection ratio	Standardized selection ratio	95% Bonferroni confidence interval
F20	Coniferous forest	0.044	0.088	0.500	0.160	0.000 [a] - 1.370
	Deciduous forest	0.033	0.077	0.429	0.138	0.000 [a] - 1.364
	Deciduous woodland	0.813	0.549	1.480	0.475	1.235 - 1.725
	Coniferous woodland	0.022	0.077	0.286	0.092	0.000 [a] - 1.221
	Shrubland	0.088	0.209	0.421	0.135	0.000 [a] - 0.947
F26	Coniferous forest	0.089	0.051	1.750	0.280	0.495 - 3.005
	Deciduous forest	0.152	0.076	2.000	0.320	0.989 - 3.011
	Deciduous woodland	0.443	0.456	0.972	0.156	0.655 - 1.289
	Coniferous woodland	0.127	0.215	0.588	0.094	0.035 - 1.142
	Shrubland	0.190	0.203	0.938	0.150	0.362 - 1.513
F58	Coniferous forest	0.044	0.062	0.706	0.172	0.101 - 1.311
	Deciduous forest	0.055	0.059	0.938	0.229	0.313 - 1.562
	Deciduous woodland	0.773	0.674	1.147	0.280	1.038 - 1.255
	Coniferous woodland	0.037	0.051	0.714	0.174	0.044 - 1.385
	Shrubland	0.092	0.154	0.595	0.145	0.230 - 0.961
M15a	Coniferous forest	0.056	0.085	0.667	0.184	0.000 [a] - 1.673
	Deciduous forest	0.070	0.099	0.714	0.198	0.000 [a] - 1.639
	Deciduous woodland	0.761	0.535	1.421	0.393	1.136 - 1.706
	Coniferous woodland	0.042	0.099	0.429	0.119	0.000 [a] - 1.353
	Shrubland	0.070	0.183	0.385	0.106	0.000 [a] - 1.030

[a] Negative lower limit was changed to 0.000.

Table 16 (continued). Selection ratios and their Bonferroni confidence intervals for land cover types used by 11 cougars on the Oquirrh Mountains, Utah, calculated for cougars that demonstrated third-order selection in prior tests.

Cougar	Land cover type	Observed proportion	Expected proportion	Selection ratio	Standardized selection ratio	95% Bonferroni confidence interval
M33	Coniferous forest	0.018	0.036	0.500	0.116	0.000 [a] - 1.764
	Deciduous forest	0.072	0.054	1.333	0.310	0.311 - 2.356
	Deciduous woodland	0.649	0.459	1.412	0.328	1.147 - 1.677
	Coniferous woodland	0.207	0.279	0.742	0.172	0.349 - 1.135
	Shrubland	0.054	0.171	0.316	0.073	0.000 [a] - 0.854

[a] Negative lower limit was changed to 0.000.

areas within his or her home range during diurnal hours. These cougars were 2 to 3 times as likely to use deciduous woodlands compared to shrublands and coniferous woodlands. Although not all individuals on the Oquirrhs were selective at a statistically significant level some use patterns were highly consistent in the entire radio-collared sample, particularly where all but 1 cougar used deciduous woodlands in greater proportion than what was available in his or her home range (Figure 12). On the Monroe site, no third-order selection for land cover types was detected in the population or in any individual cougar (Table 17, Figure 13).

Edge. – The random home range simulation indicated that the Oquirrhs study site contained more edge habitat compared to the Monroe site (Figure 14, Figure 15). Cougars on both study sites selected home ranges with significantly more edge compared to availability in the study area (Table 18, Table 19). Cougar home ranges on the Oquirrhs included a higher density of edge on average than cougar home ranges on the Monroe site, and edge density was less variable among cougars on the Oquirrhs.

Slope. – Proportional availability of slope classes differed on the 2 study sites. Results from the random home range simulations indicated that the Oquirrh Mountains contained greater proportions of steep slopes (40 - 70%) and smaller proportions of gentle slopes (< 20%) compared to Monroe Mountain (Table 20, Table 21). Although these study site differences existed, cougar home ranges on both sites included larger proportions of moderate (20 - 40%) and steep (40 - 70%) slopes compared to random home ranges, and smaller proportions of gentle slopes (Figure 16, Figure 17). Rugged slopes (> 70%) were rare on both study sites and cougars used them in proportion to availability at the second order.

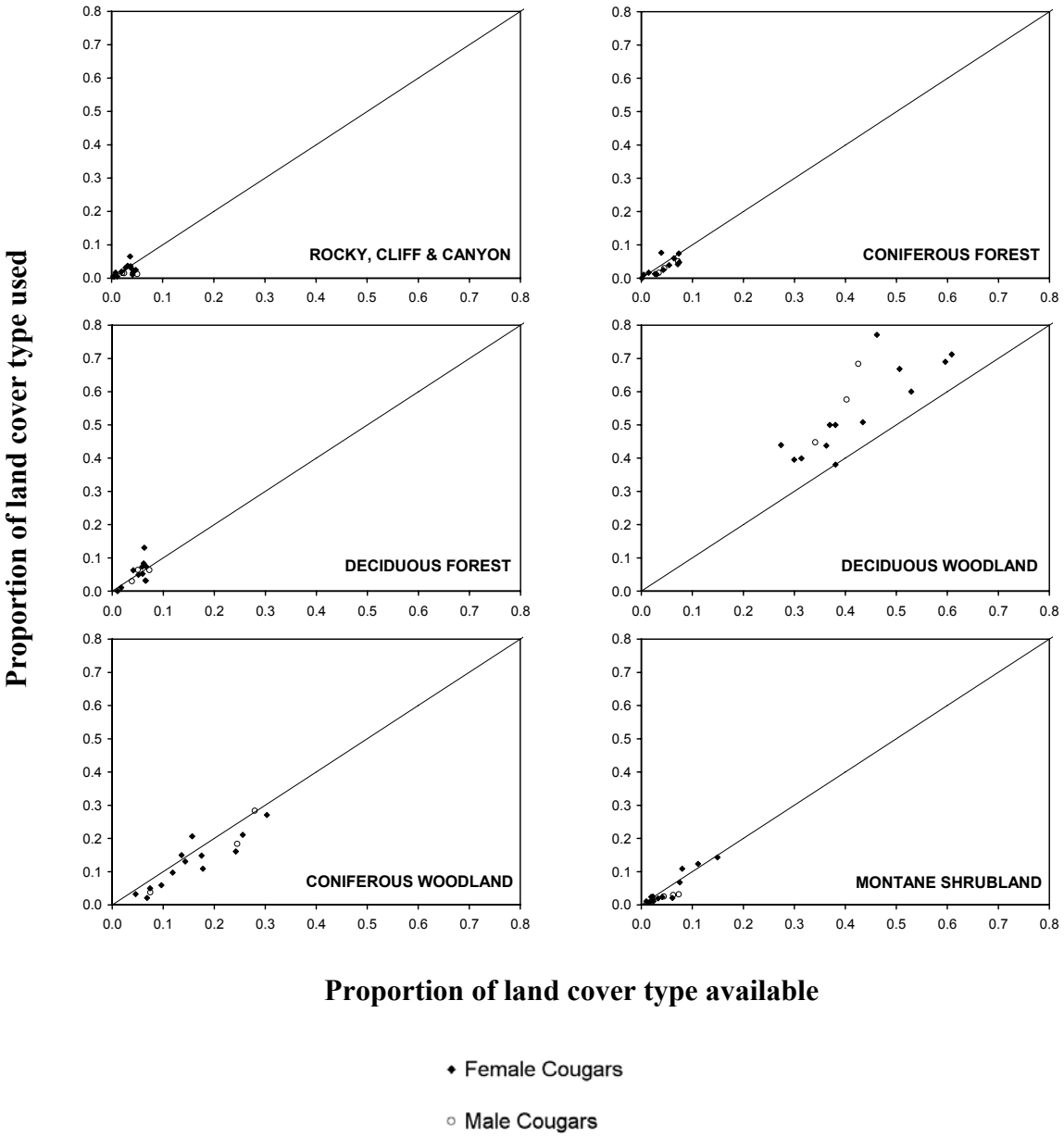

Figure 12. Third-order selection by 13 female and 3 male cougars for 11 land cover types in the Oquirrh Mountains, Utah. Points represent resource use (quantified by the individual's buffered radiolocations) versus availability (quantified by the individual's 95% fixed kernel home range) compared to a one-to-one correspondence line. Agriculture is not shown because it rarely occurred in cougar home ranges.

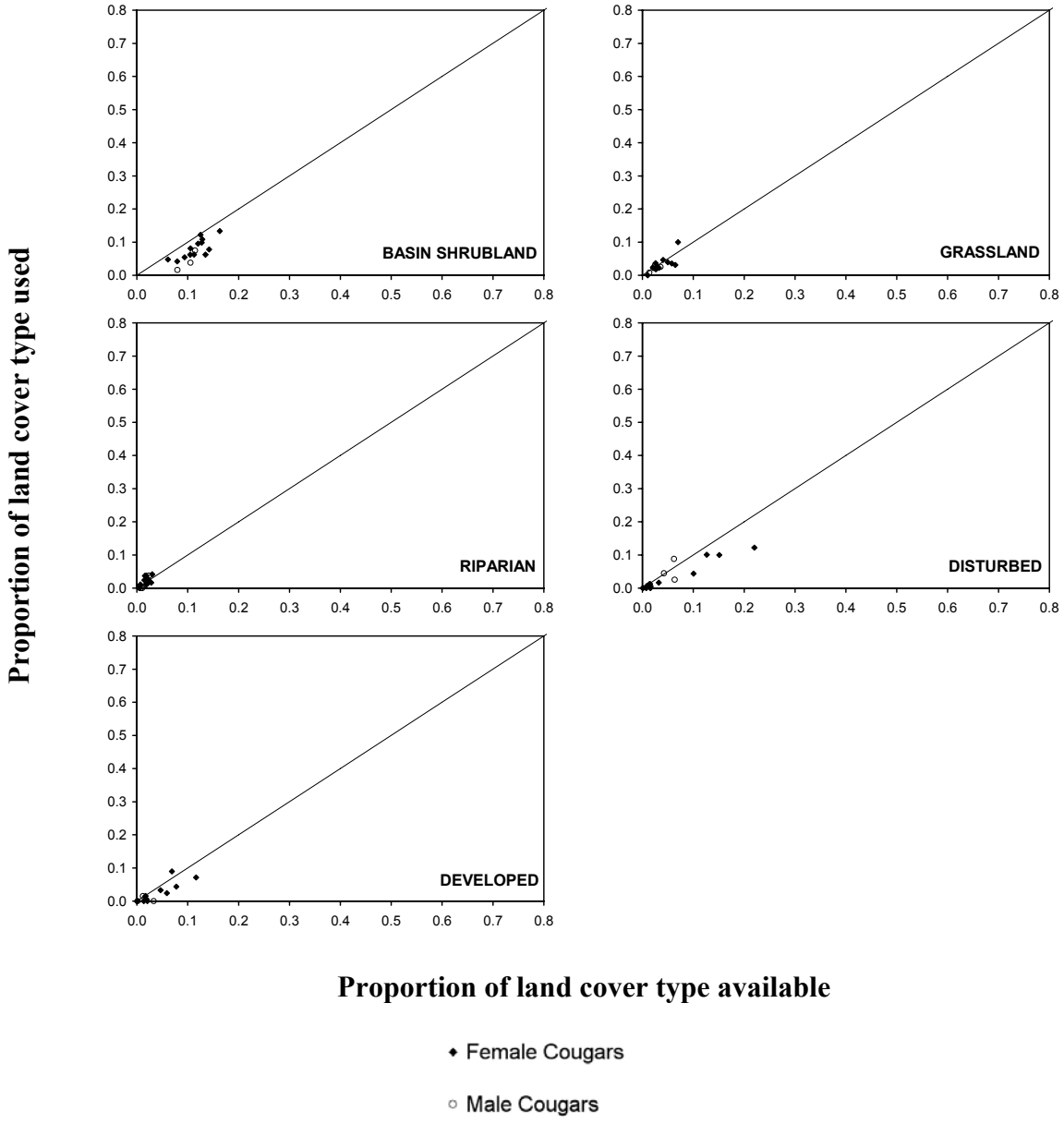

Figure 12 (continued). Third-order selection by 13 female and 3 male cougars for 11 land cover types in the Oquirrh Mountains, Utah.

Table 17. Number of radiolocations observed and number expected in 5 land cover types for 20 female cougars on Monroe Mountain, Utah. Third-order selection was tested at the individual level using exact chi-square goodness-of-fit tests, and an overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Conif. forest		Decid. forest		Decid. woodl		Conif. woodl.		Shrubland		X^2 statistic	df	Exact p-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp			
F01	5	5	14	9	6	4	8	9	10	16	6.14	4	0.186
F03	7	10	17	15	3	3	13	11	16	17	1.59	4	0.814
F04	7	7	15	12	1	1	9	7	11	16	2.88	4	0.569
F05	4	3	7	4	1	1	20	28	35	31	5.39	4	0.235
F06	3	3	6	7	1	1	15	10	14	18	3.53	4	0.457
F08	14	9	7	6	3	1	21	22	15	22	9.22	4	0.060
F09	9	6	4	5	2	2	13	13	2	4	2.70	4	0.616
F12	31	24	24	23	10	10	23	30	10	11	3.81	4	0.434
F16	10	9	9	8	2	2	14	12	12	16	1.57	4	0.816
F17	2	2	4	2	0	0	13	11	10	14	3.51	3	0.326
F26a	9	7	7	6	2	1	5	6	7	10	2.80	4	0.595
F30	2	3	1	2	3	2	14	12	8	9	1.78	4	0.790
F32b	0	0	0	0	3	4	33	31	9	10	0.48	2	0.813
F35	3	3	3	3	1	0	15	13	14	17	0.84	3	0.841
F36	1	1	4	3	1	1	24	23	13	15	0.64	4	0.960
F40	2	3	10	8	4	3	12	10	11	15	2.63	4	0.623
F43	3	4	3	3	2	2	17	14	10	12	1.23	4	0.875
F49	7	5	3	3	1	1	11	13	15	15	1.11	4	0.922
F52	1	2	1	2	1	1	15	12	10	11	1.84	4	0.772
F53	1	1	2	3	1	1	14	14	17	16	0.40	4	0.986
Population											54.08	76	0.984

[a] Obs = observed

[b] Exp = expected

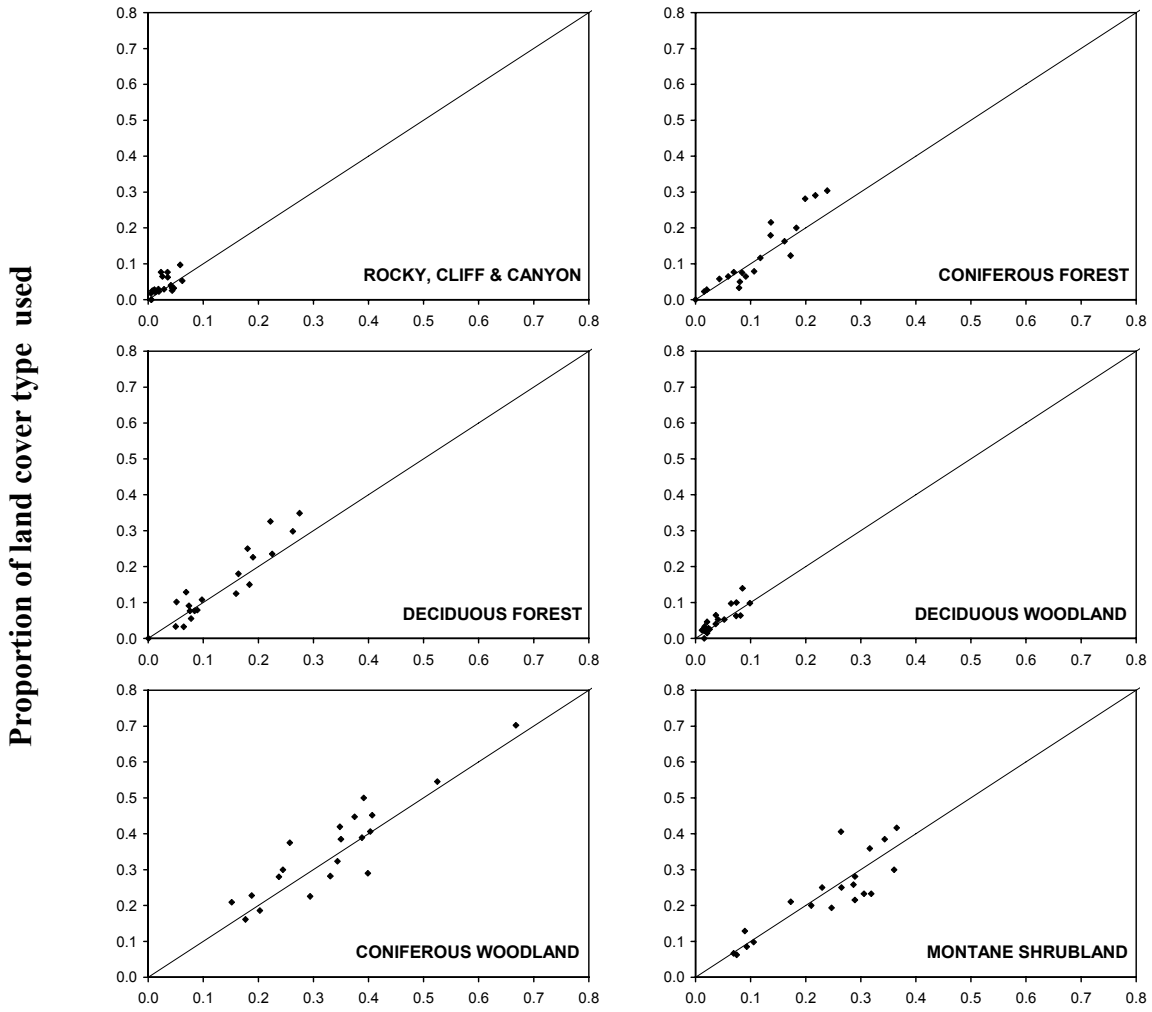

Figure 13. Third-order selection by 20 female cougars for 7 land cover types on Monroe Mountain, Utah. For each land cover type, proportional availability was quantified by the individual's 95% fixed kernel home range, and use was quantified by the individual's buffered radiolocations. Line indicates where use and availability would be equal. Grassland, riparian, disturbed, developed, and agriculture types are not shown because they rarely occurred in cougar home ranges.

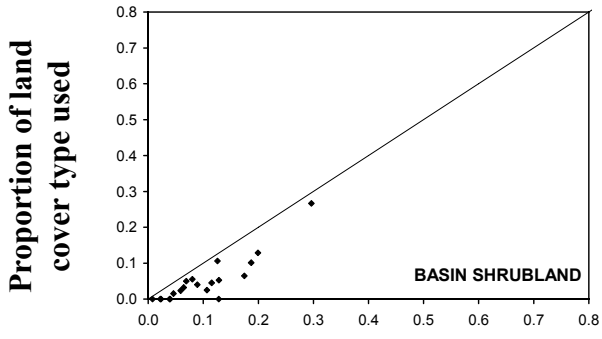

Figure 13 (continued). Third-order selection by 20 female cougars for 7 land cover types on Monroe Mountain, Utah.

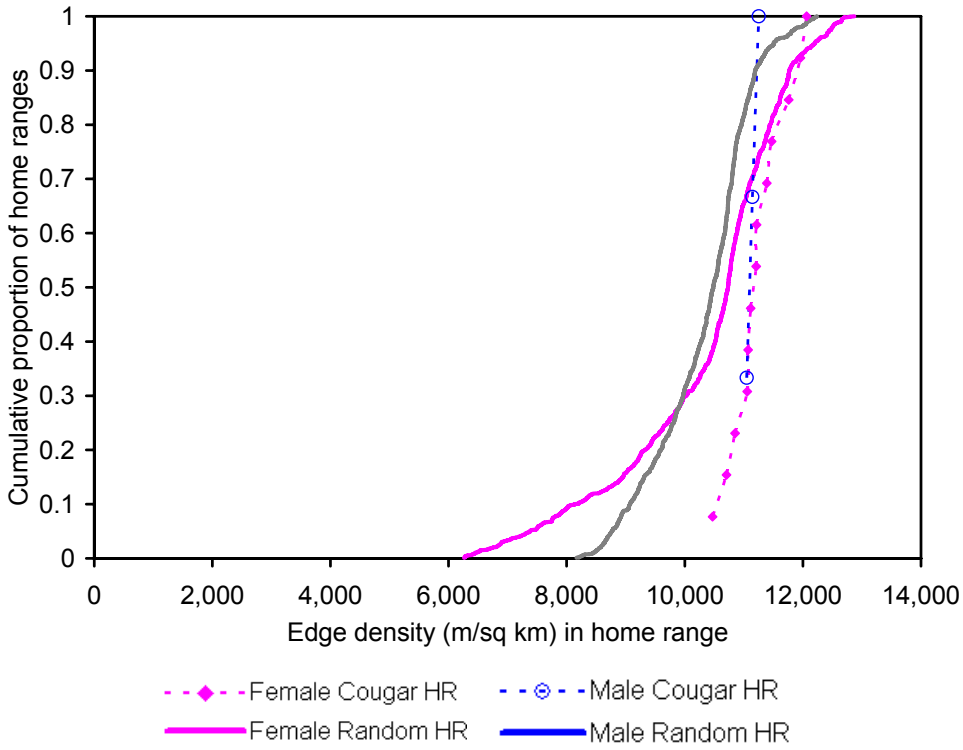

Figure 14. Cumulative distribution functions for edge density in 3 male and 13 female cougar home ranges compared to density in 1,000 randomly placed home ranges on the Oquirrh Mountains, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

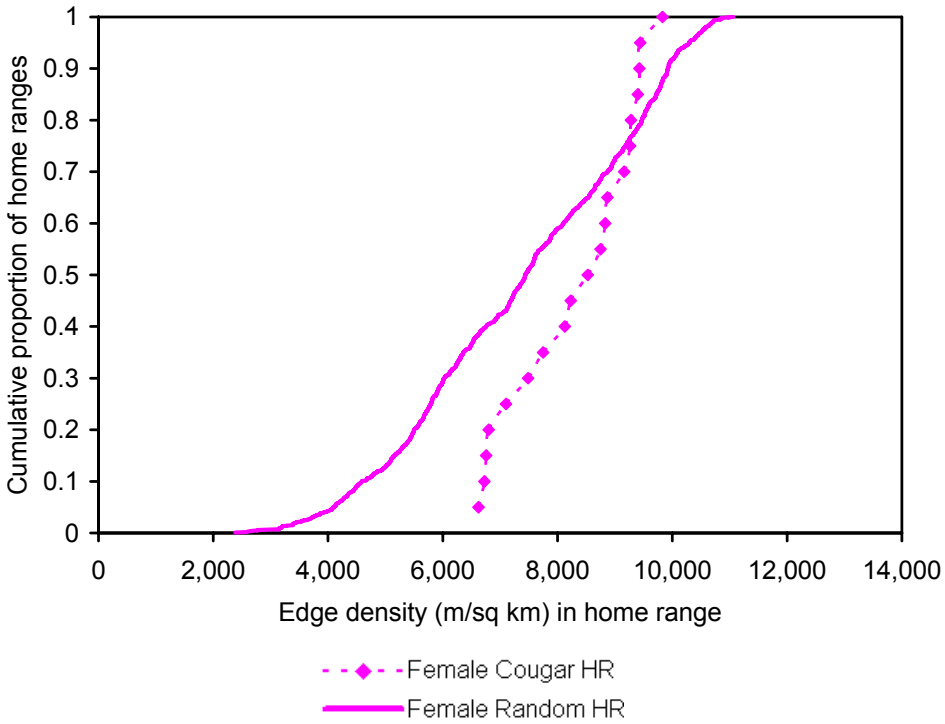

Figure 15. Cumulative distribution functions for edge density in 20 female cougar home ranges compared to density in 1,000 randomly placed home ranges on Monroe Mountain, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

Table 18. Edge density in 95% fixed kernel home ranges of 3 male and 13 female cougars on the Oquirrh Mountains, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Edge density (m/km^2)
Females	
F06	11,957
F12	11,216
F13	11,389
F18	11,073
F19	11,759
F20	11,472
F26	11,208
F53	12,065
F56	10,852
F58	10,472
F59	10,705
F62	11,060
F68	11,115
Cougar mean	11,257
Cougar SD	469
Random mean	10,375
Random SD	1,383
$D_{n=13}$	0.445
P-value	0.012
Males	
M15a	11,252
M16	11,144
M33	11,050
Cougar mean	11,149
Cougar SD	101
Random mean	10,325
Random SD	821

Table 19. Edge density in 95% fixed kernel home ranges of 20 female cougars on Monroe Mountain, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Edge Density (m/km^2)
F01	6,622
F03	6,726
F04	6,756
F05	6,799
F06	7,100
F08	7,485
F09	7,747
F12	8,127
F16	8,230
F17	8,526
F26a	8,749
F30	8,830
F32b	8,870
F35	9,161
F36	9,262
F40	9,279
F43	9,400
F49	9,427
F52	9,441
F53	9,829
Cougar mean	8,318
Cougar SD	1,075
Random mean	7,388
Random SD	1,993
$D_{n=20}$	0.384
P-value	0.006

Table 20. Proportions of slope classes in 95% fixed kernel home ranges of 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Second-order selection was tested only for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test

Cougar	Gentle (< 20%)	Moderate (20 - 40%)	Steep (40 - 70%)	Rugged (> 70%)
Females				
F06	0.331	0.308	0.337	0.024
F12	0.362	0.428	0.208	0.002
F13	0.139	0.434	0.401	0.026
F18	0.243	0.461	0.292	0.003
F19	0.308	0.429	0.260	0.004
F20	0.162	0.336	0.465	0.038
F26	0.191	0.404	0.393	0.013
F53	0.304	0.334	0.328	0.034
F56	0.290	0.306	0.367	0.037
F58	0.170	0.392	0.416	0.022
F59	0.214	0.297	0.428	0.061
F62	0.296	0.360	0.326	0.019
F68	0.286	0.339	0.352	0.022
Cougar mean	0.254	0.371	0.352	0.023
Cougar SD	0.072	0.056	0.071	0.017
Random mean	0.374	0.313	0.288	0.026
Random SD	0.193	0.072	0.158	0.032
$D_{n=13}$	0.547	0.430	0.451	0.288
P-value	< 0.001	0.017	0.011	0.237
Adjusted p-value	0.004	0.023	0.022	0.237
Males				
M15a	0.174	0.300	0.457	0.070
M16	0.287	0.394	0.299	0.021
M33	0.241	0.425	0.325	0.009
Cougar mean	0.234	0.373	0.360	0.033
Cougar SD	0.057	0.065	0.085	0.032
Random mean	0.413	0.277	0.280	0.030
Random SD	0.103	0.051	0.089	0.023

Table 21. Proportions of slope classes in 95% fixed kernel home ranges of 20 female cougars on Monroe Mountain, Utah. Second-order selection was tested for female cougars by comparing a Cumulative Distribution Function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Gentle (< 20%)	Moderate (20 - 40%)	Steep (40 - 70%)	Rugged (> 70%)
F01	0.485	0.369	0.133	0.013
F03	0.407	0.447	0.143	0.003
F04	0.529	0.339	0.125	0.008
F05	0.339	0.352	0.221	0.028
F06	0.490	0.347	0.154	0.008
F08	0.327	0.367	0.263	0.044
F09	0.186	0.310	0.386	0.119
F12	0.303	0.317	0.282	0.097
F16	0.326	0.338	0.282	0.053
F17	0.429	0.342	0.204	0.025
F26a	0.341	0.287	0.309	0.063
F30	0.263	0.336	0.340	0.061
F32b	0.570	0.317	0.105	0.007
F35	0.409	0.364	0.210	0.017
F36	0.330	0.428	0.227	0.015
F40	0.463	0.386	0.147	0.005
F43	0.299	0.297	0.339	0.065
F49	0.252	0.373	0.319	0.056
F52	0.360	0.321	0.259	0.060
F53	0.490	0.347	0.156	0.008
Cougar mean	0.383	0.349	0.230	0.038
Cougar SD	0.101	0.040	0.084	0.033
Random mean	0.492	0.299	0.179	0.030
Random SD	0.101	0.059	0.060	0.021
$D_{n=20}$	0.418	0.443	0.352	0.261
P-value	0.002	< 0.001	0.016	0.138
Adjusted p-value	0.004	0.004	0.021	0.138

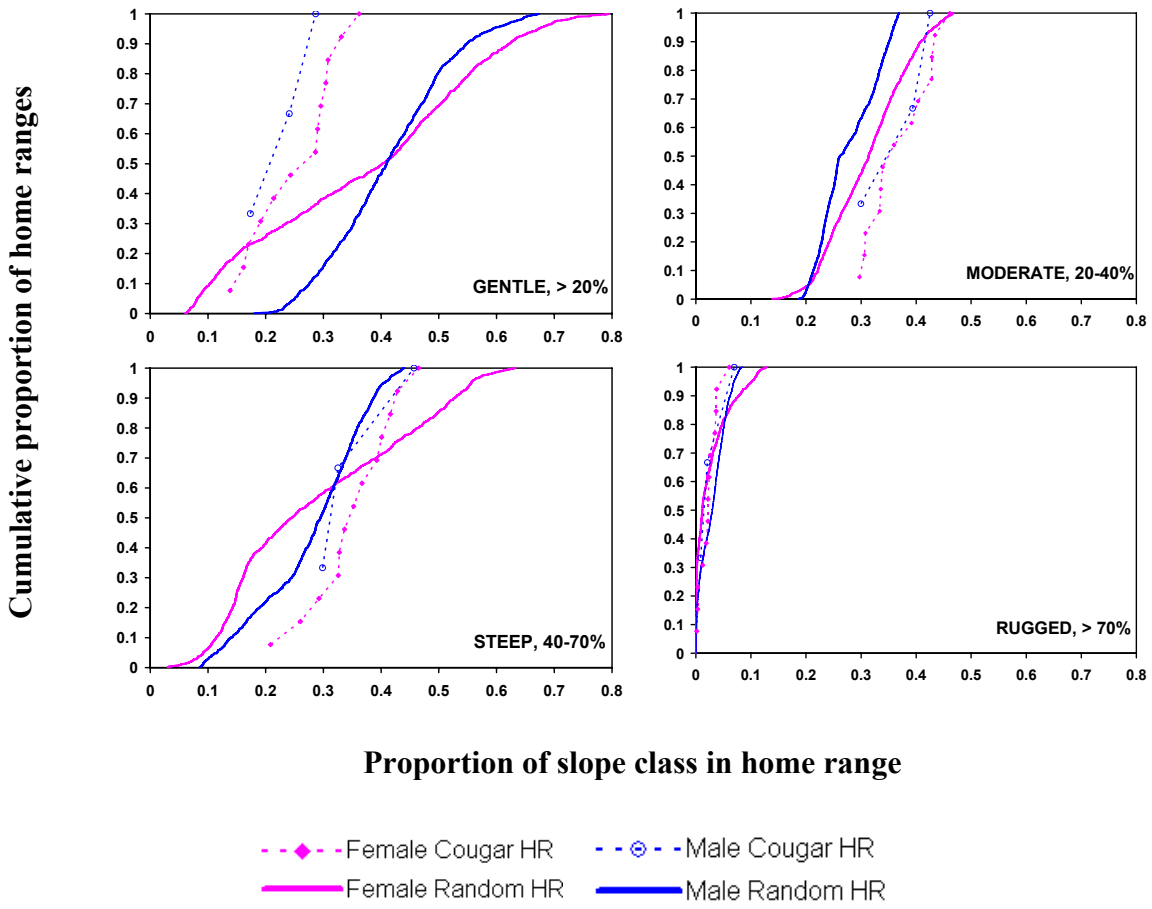

Figure 16. Cumulative distribution functions for proportion of slope classes in 13 female and 3 male cougar home ranges compared to proportion in 1,000 randomly placed home ranges on the Oquirrh Mountains, Utah. The random home ranges were circles with area equal to the mean cougar home range size for each sex on the study site.

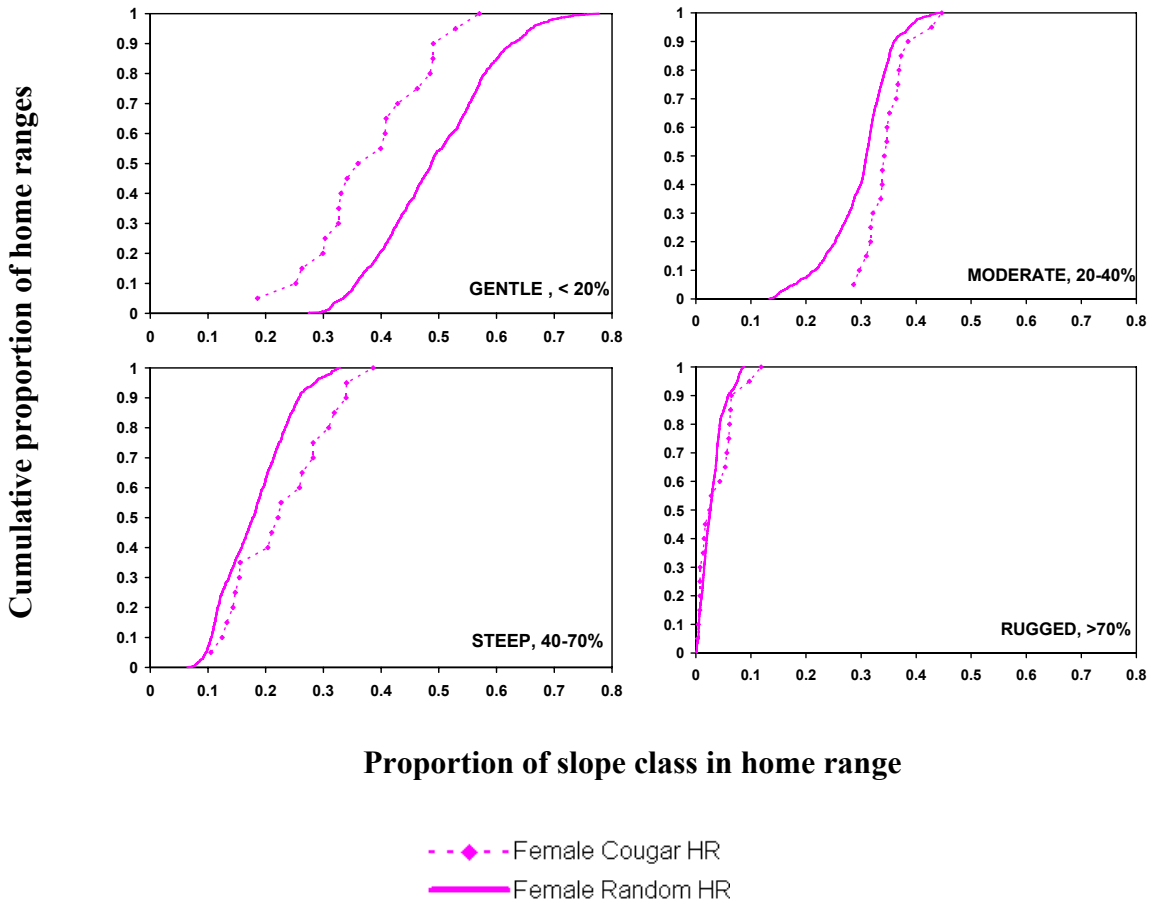

Figure 17. Cumulative distribution functions for proportion of slope classes in 20 female cougar home ranges compared to proportion in 1,000 randomly placed home ranges on Monroe Mountain, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

On the Oquirrhs site, 5 cougars used slope classes selectively at the third order (Table 22). Specifically, these cougars avoided gentle slopes and selected steep slopes when using areas within their home ranges (Table 23). Though not statistically significant for all cougars, in general this pattern held for the population (Figure 18). On the Monroe site, no statistically significant difference was detected in individual cougar use versus availability of slope classes at the third order (Table 24). However, as on the Oquirrhs site, most cougars tended to use moderate and steep slopes in their home range and avoid gentle slopes (Figure 19).

Landform. – Cougar selection of landforms at the second order was consistent between the Oquirrh Mountains and Monroe Mountain. Home ranges on both sites included larger proportions of canyons/drainages, steep hillsides, and ridges/hilltops compared to availability on the study site, and smaller proportions of valley basins (Table 25, Table 26, Figure 20, Figure 21). Gentle hillsides on both study sites were used in proportion to availability at the second order.

At the third order, 6 cougars on the Oquirrhs site selectively used land forms (Table 27). The majority of these cougars used canyons/drainages within their home range more than expected (Table 28). In the plots of use versus availability for all sampled cougars on the Oquirrhs, cougars also appeared to avoid valley basins and flats within their home range (Figure 22). No cougars on the Monroe site used landforms selectively at the third order (Table 29). However, when considering proportional use by all sampled cougars on Monroe, results were similar to those from the Oquirrhs; namely, there appeared to be a tendency to use canyons/drainages more than expected and avoid valleys and flats within their home ranges (Figure 23).

Table 22. Number of radiolocations observed and number expected in 4 slope classes for 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Third-order selection was tested at the individual level using chi-square goodness-of-fit tests, and an overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Gentle (<20%)		Moderate (20-40%)		Steep (40-70%)		Rugged (>70%)		X^2 Statistic	df	P-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp			
F06	86	89	107	83	73	80	2	6	12.92	3	0.005
F12	45	70	93	83	54	40	0	0	15.03	2	<0.001
F13	8	8	27	27	27	26	1	2	0.54	3	0.910
F18	61	104	200	197	163	125	3	1	33.38	3	<0.001
F19	31	59	79	82	81	50	1	1	32.62	3	<0.001
F20	8	15	37	32	49	45	2	4	5.40	3	0.145
F26	4	18	28	37	58	36	2	1	27.52	3	<0.001
F53	16	25	32	27	31	26	2	3	5.46	3	0.141
F56	9	12	17	13	14	15	1	1	2.05	3	0.563
F58	39	52	116	120	142	127	9	7	5.73	3	0.126
F59	14	20	30	24	37	35	3	5	4.21	3	0.239
F62	12	18	21	22	25	19	2	1	4.94	3	0.176
F68	40	46	60	54	57	56	3	4	1.72	3	0.633
M15a	11	14	33	24	32	36	3	5	5.26	3	0.154
M16	11	19	31	26	24	20	1	2	5.63	3	0.131
M33	22	30	61	53	41	41	1	1	3.34	3	0.342
Population									165.75	47	<0.001

[a] Obs = observed

[b] Exp = expected

Table 23. Selection ratios and their Bonferroni confidence intervals for slope classes used by 5 cougars on the Oquirrh Mountains, Utah, calculated only for cougars that demonstrated third-order selection in prior tests. Cougar use of a slope class was significantly different from availability if the confidence interval did not include the value one.

Cougar	Slope class	Observed proportion	Expected proportion	Selection ratio	Standardized selection ratio	95% Bonferroni confidence interval
F06	Gentle	0.321	0.331	0.969	0.287	0.753 - 1.186
	Moderate	0.399	0.308	1.296	0.383	1.067 - 1.524
	Steep	0.272	0.337	0.809	0.239	0.595 - 1.024
	Rugged	0.007	0.024	0.307	0.091	0.000 [a] - 1.275
F12	Gentle	0.233	0.362	0.644	0.106	0.406 – 0.883
	Moderate	0.482	0.428	1.126	0.186	0.918 – 1.333
	Steep	0.280	0.208	1.343	0.221	0.993 – 1.694
	Rugged	0.005	0.002	2.953	0.487	0.000 [a] - 7.241
F18	Gentle	0.143	0.243	0.588	0.118	0.374 – 0.801
	Moderate	0.468	0.461	1.015	0.204	0.885 – 1.146
	Steep	0.382	0.292	1.306	0.262	1.118 – 1.494
	Rugged	0.007	0.003	2.068	0.415	0.000 [a] – 4.138
F19	Gentle	0.161	0.308	0.524	0.114	0.254 – 0.794
	Moderate	0.411	0.429	0.960	0.209	0.752 – 1.168
	Steep	0.422	0.260	1.623	0.353	1.319 – 1.927
	Rugged	0.005	0.003	1.488	0.324	0.000 [a] – 4.530
F26	Gentle	0.043	0.191	0.227	0.052	0.000 [a] – 0.762
	Moderate	0.304	0.404	0.754	0.174	0.438 – 1.071
	Steep	0.630	0.393	1.606	0.371	1.282 – 1.930
	Rugged	0.022	0.012	1.740	0.402	0.000 [a] – 4.056

[a] Negative lower limit was changed to 0.000.

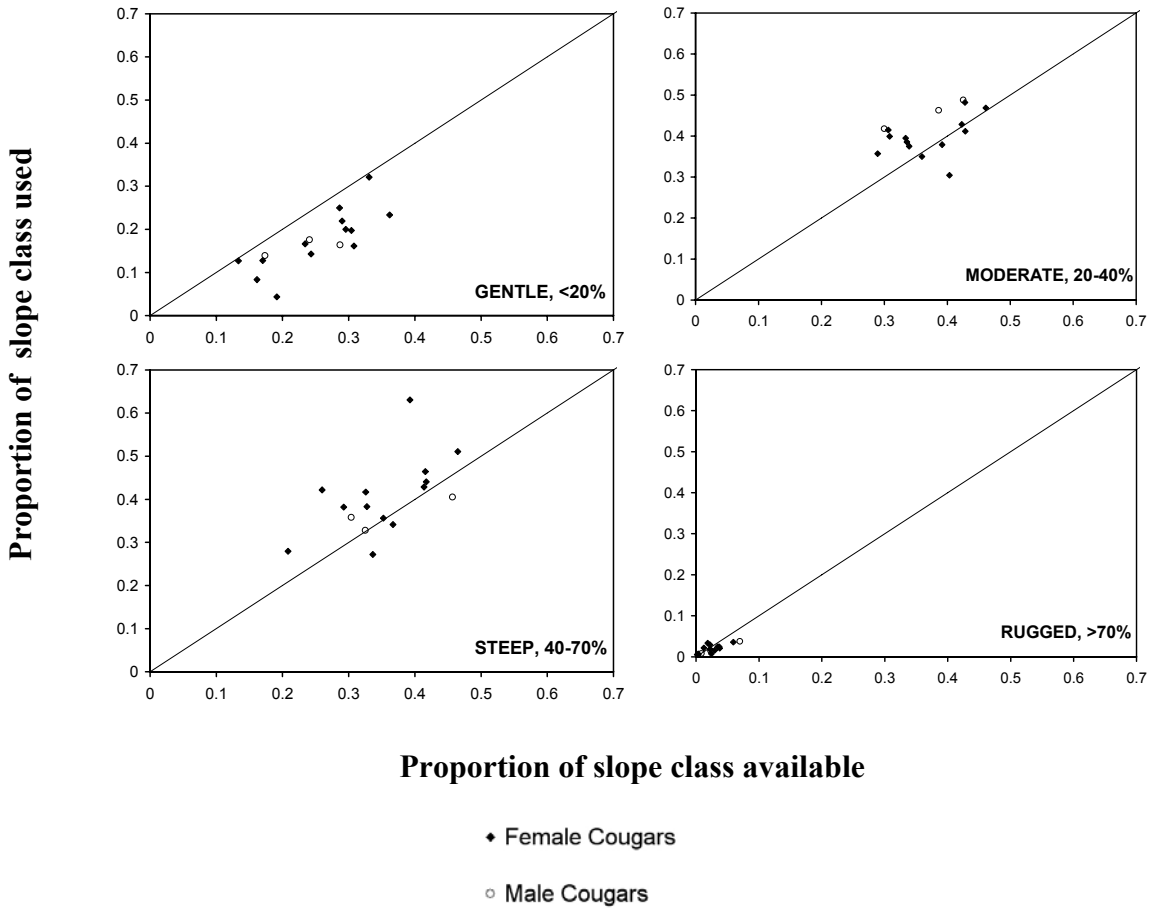

Figure 18. Third-order selection by 3 male and 13 female cougars for 4 slope classes on the Oquirrh Mountains, Utah. For each land cover type, proportional availability was quantified by the individual's 95% fixed kernel home range, and use was quantified by the individual's buffered radiolocations. Line indicates where use and availability would be exactly equal.

Table 24. Number of radiolocations observed and number expected in 4 slope classes for 20 female cougars Monroe Mountain, Utah. Third-order selection was tested at the individual level using chi-square goodness-of-fit tests, and an overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Gentle (<20%)		Moderate (20-40%)		Steep (40-70%)		Rugged (>70%)		X^2 Statistic	df	P-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp			
F01	14	21	20	16	9	6	0	0	4.83	2	0.089
F03	16	23	27	26	14	8	NIHR		6.67	2	0.036
F04	20	23	18	15	5	5	0	0	0.99	2	0.609
F05	25	28	25	24	17	15	2	2	0.63	3	0.890
F06	16	20	14	14	9	6	1	0	2.30	2	0.317
F08	15	21	23	24	22	17	5	3	4.56	3	0.207
F09	3	6	10	10	13	12	6	4	2.58	3	0.460
F12	25	31	28	32	33	29	16	10	5.81	3	0.121
F16	11	16	19	17	18	14	2	3	3.27	3	0.351
F17	8	13	13	11	9	6	1	1	3.79	3	0.285
F26a	7	10	9	9	12	10	3	2	1.80	3	0.615
F30	6	8	11	10	11	11	3	2	1.10	3	0.777
F32b	24	27	17	15	5	5	NIHR		0.60	2	0.741
F35	8	16	16	14	13	8	2	1	8.41	3	0.038
F36	11	14	20	19	12	10	1	1	1.10	3	0.778
F40	11	19	19	15	10	6	0	0	7.10	2	0.029
F43	12	11	12	11	12	13	3	1	0.59	3	0.898
F49	6	10	15	15	15	12	3	2	2.85	3	0.415
F52	9	11	11	9	8	8	2	2	0.81	3	0.848
F53	14	18	12	12	9	6	NIHR		2.39	2	0.303
Population									62.19	53	0.182

[a] Obs = observed

[b] Exp = expected

[c] NIHR = "not in home range"; the slope class did not occur in the cougar's home range and therefore was not available for third-order selection

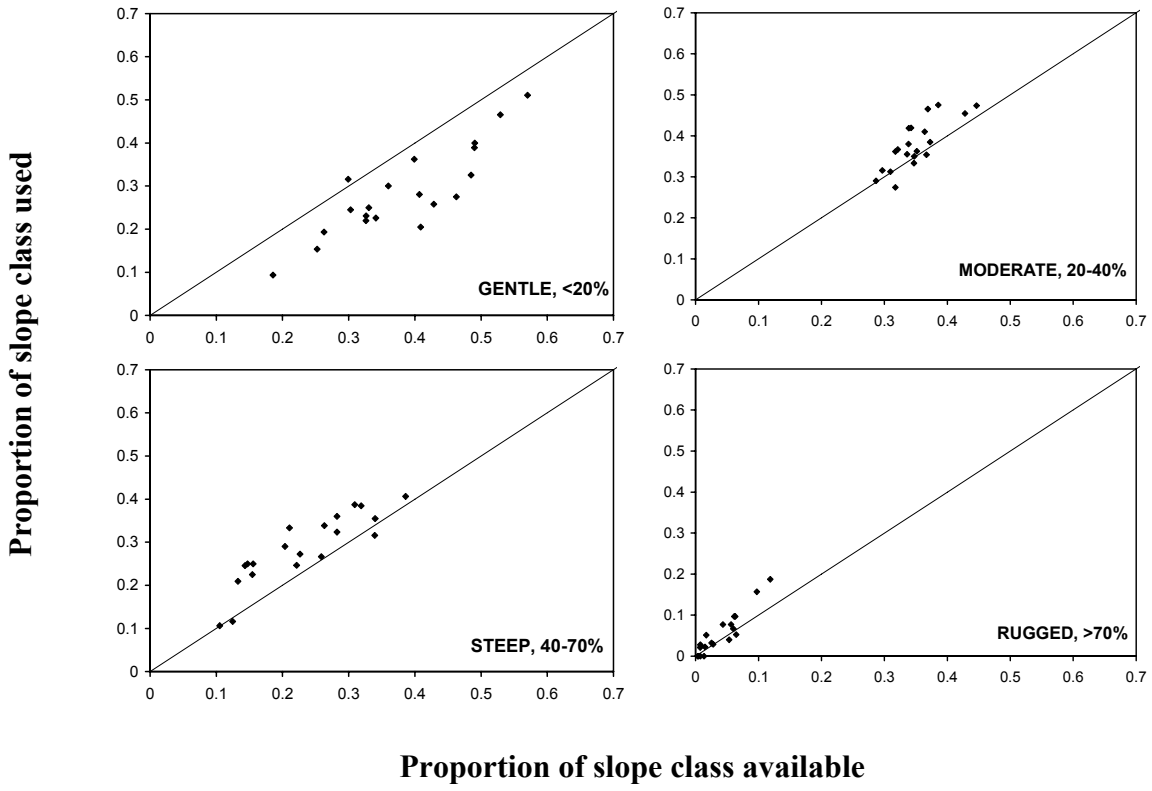

Figure 19. Third-order selection by 20 female cougars for 4 slope classes on Monroe Mountain, Utah. For each land cover type, proportional availability was quantified by the individual's 95% fixed kernel home range, and use was quantified by the individual's buffered radiolocations. Line indicates where use and availability would be perfectly equal.

Table 25. Proportions of landform classes in 95% fixed kernel home ranges of 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Second-order selection was tested for female cougars by comparing a cumulative distribution function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Valley basins, flats	Canyons, drainages	Gentle hillsides	Steep hillsides	Ridges, hilltops
Females					
F06	0.099	0.179	0.460	0.078	0.184
F12	0.064	0.169	0.480	0.096	0.190
F13	0.004	0.260	0.327	0.171	0.238
F18	0.012	0.181	0.443	0.120	0.243
F19	0.051	0.172	0.477	0.114	0.186
F20	0.021	0.259	0.303	0.181	0.236
F26	0.022	0.223	0.362	0.156	0.237
F53	0.079	0.206	0.387	0.130	0.198
F56	0.062	0.203	0.432	0.101	0.202
F58	0.013	0.247	0.363	0.156	0.221
F59	0.070	0.241	0.304	0.155	0.231
F62	0.066	0.212	0.378	0.156	0.189
F68	0.068	0.190	0.482	0.081	0.179
Cougar mean	0.048	0.211	0.400	0.130	0.210
Cougar SD	0.030	0.033	0.066	0.035	0.024
Random mean	0.155	0.179	0.375	0.109	0.181
Random SD	0.140	0.074	0.091	0.056	0.062
$D_{n=13}$	0.545	0.501	0.230	0.385	0.535
P-value	0.001	0.003	0.504	0.045	0.001
Adjusted p-value	0.003	0.005	0.504	0.056	0.003
Males					
M15a	0.024	0.251	0.338	0.147	0.239
M16	0.050	0.205	0.419	0.121	0.206
M33	0.024	0.215	0.406	0.133	0.221
Cougar mean	0.033	0.224	0.388	0.134	0.222
Cougar SD	0.015	0.024	0.043	0.013	0.017
Random mean	0.208	0.170	0.343	0.106	0.172
Random SD	0.084	0.039	0.045	0.033	0.031

Table 26. Proportions of landform classes in 95% fixed kernel home ranges of 20 female cougars on Monroe Mountain, Utah. Second-order selection was tested for female cougars by comparing a cumulative distribution function (CDF) generated from cougar home ranges to a CDF from 1,000 random home ranges using a Kolmogorov-Smirnov goodness-of-fit test.

Cougar	Valley basins, flats	Canyons, drainages	Gentle hillsides	Steep hillsides	Ridges, hilltops
F01	0.125	0.125	0.449	0.150	0.149
F03	0.076	0.129	0.453	0.181	0.162
F04	0.174	0.129	0.456	0.108	0.132
F05	0.099	0.172	0.374	0.172	0.182
F06	0.143	0.155	0.434	0.117	0.151
F08	0.056	0.193	0.342	0.198	0.211
F09	0.017	0.243	0.296	0.202	0.242
F12	0.051	0.204	0.353	0.170	0.222
F16	0.048	0.196	0.341	0.217	0.198
F17	0.138	0.159	0.387	0.148	0.168
F26a	0.079	0.211	0.262	0.246	0.203
F30	0.039	0.217	0.271	0.251	0.222
F32b	0.163	0.118	0.501	0.100	0.118
F35	0.104	0.159	0.403	0.157	0.178
F36	0.030	0.177	0.417	0.183	0.193
F40	0.146	0.130	0.416	0.151	0.156
F43	0.045	0.208	0.291	0.245	0.211
F49	0.019	0.226	0.309	0.212	0.235
F52	0.064	0.178	0.346	0.209	0.202
F53	0.146	0.135	0.459	0.117	0.143
Cougar mean	0.088	0.173	0.378	0.177	0.184
Cougar SD	0.051	0.038	0.070	0.046	0.035
Random mean	0.200	0.137	0.369	0.145	0.150
Random SD	0.111	0.035	0.066	0.038	0.034
$D_{n=20}$	0.530	0.874	0.942	0.784	0.771
P-value	< 0.001	0.011	0.520	0.037	0.005
Adjusted p-value	0.001	0.019	0.520	0.046	0.012

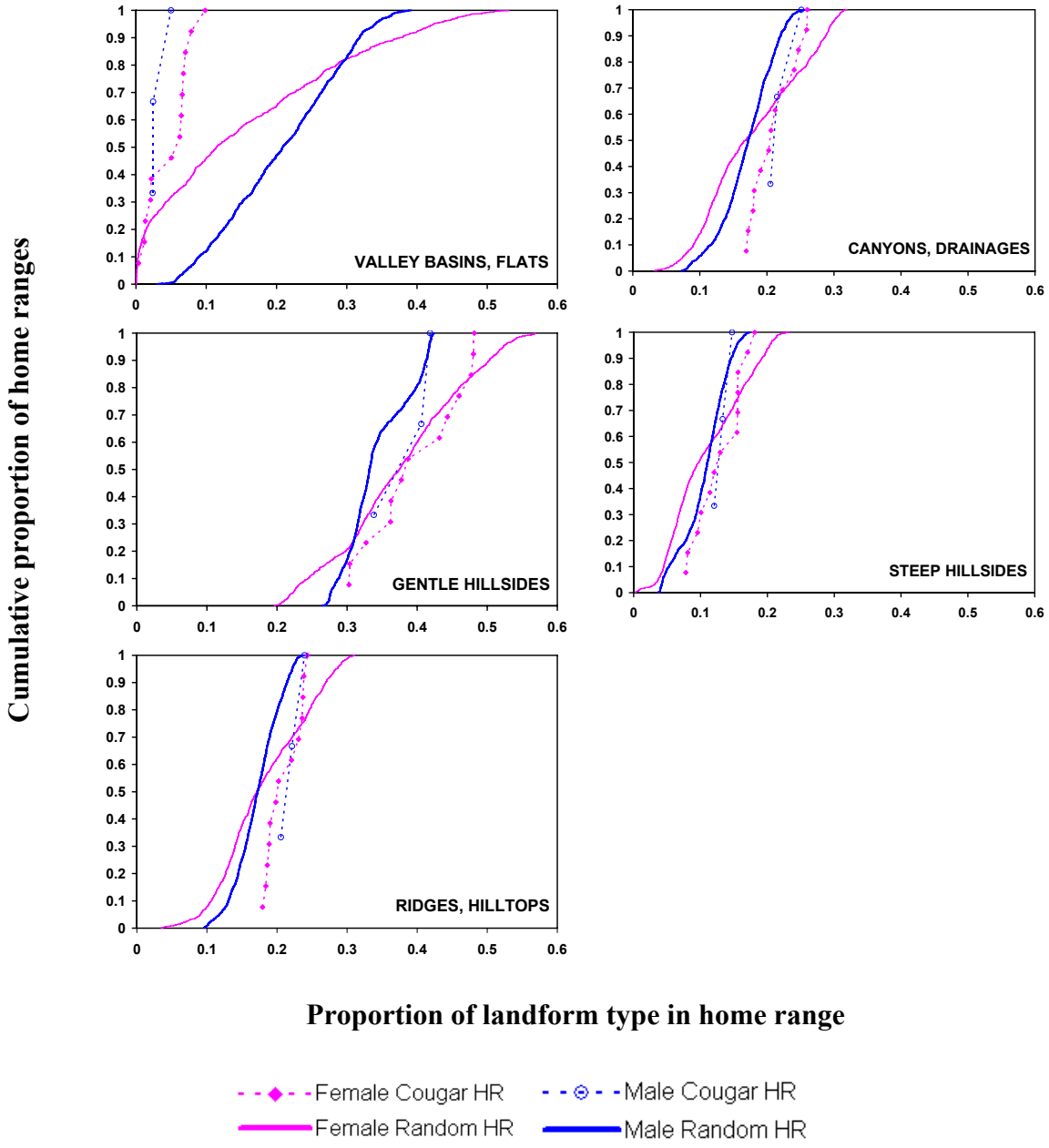

Figure 20. Cumulative distribution functions for proportion of land form types in 13 female and 3 male cougar home ranges compared to proportion in 1,000 randomly placed home ranges on the Oquirrh Mountains, Utah. The random home ranges were circles with area equal to the mean cougar home range size for each sex on the study site.

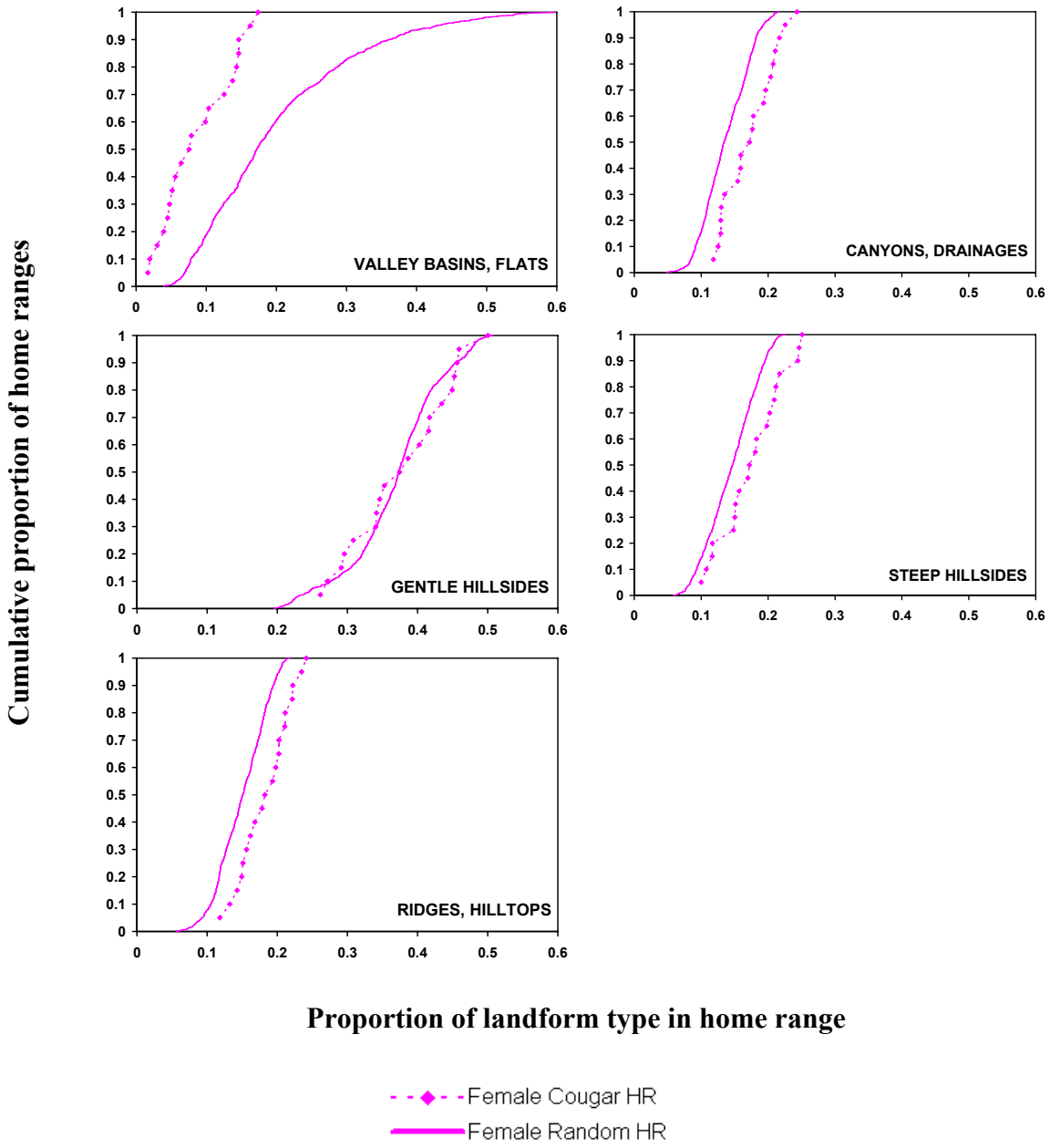

Figure 21. Cumulative distribution functions for proportion of landform types in 20 female cougar home ranges compared to proportion in 1,000 randomly placed home ranges on Monroe Mountain, Utah. The random home ranges were circles with area equal to the mean female cougar home range size on the study site.

Table 27. Number of radiolocations observed and number expected by landform class in home ranges of 13 female and 3 male cougars on the Oquirrh Mountains, Utah. Third-order selection was tested at the individual level using chi-square goodness-of-fit tests, and an overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Valley basins, flats		Canyons, drainages		Gentle hillsides		Steep hillsides		Ridges, hilltops		X^2 Statistic	df	P-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp			
F06	16	27	53	49	158	126	17	22	31	51	21.92	4	<0.001
F12	1	4	16	12	26	33	12	6	13	13	11.07	4	0.026
F13	0	0	16	17	19	20	13	11	15	15	0.47	3	0.925
F18	1	5	124	77	162	189	52	51	87	104	38.54	4	<0.001
F19	3	10	49	33	79	92	24	22	38	36	14.79	4	0.005
F20	0	2	23	25	33	29	18	18	23	23	21.71	4	0.607
F26	0	2	21	21	27	33	21	14	23	22	6.64	4	0.156
F53	2	6	19	17	27	31	17	10	16	16	8.32	4	0.081
F56	1	3	8	8	21	18	3	4	8	8	2.08	4	0.720
F58	3	4	102	76	103	111	45	48	54	68	12.79	4	0.012
F59	2	7	23	20	22	25	20	13	17	19	8.36	4	0.079
F62	2	4	13	13	21	23	9	9	15	11	2.63	4	0.622
F68	5	11	34	30	82	77	10	13	29	29	4.82	4	0.306
M15a	0	2	31	20	28	27	9	11	11	19	11.82	4	0.019
M16	1	3	17	14	31	28	4	8	14	14	4.30	4	0.367
M33	1	3	32	27	55	51	15	16	22	28	3.92	4	0.4168
Population											155.18	63	<0.001

[a] Obs = observed

[b] Exp = expected

Table 28. Selection ratios and their Bonferroni confidence intervals for landforms used by 6 cougars on the Oquirrh Mountains, Utah, calculated only for cougars that demonstrated third-order selection in prior tests. Cougar use of a landform was significantly different from availability if the confidence interval did not include the value 1.

Cougar	Landform	Observed proportion	Expected proportion	Selection ratio	Standardized selection ratio	95% Bonferroni confidence interval
F06	Valley basins, flats	0.058	0.099	0.591	0.137	0.115 – 1.067
	Canyons, drainages	0.193	0.179	1.074	0.249	0.738 – 1.411
	Gentle hillsides	0.575	0.460	1.249	0.289	1.079 – 1.420
	Steep hillsides	0.062	0.078	0.791	0.183	0.251 – 1.332
	Ridges, hilltops	0.113	0.184	0.612	0.142	0.281 – 0.944
F12	Valley basins, flats	0.015	0.064	0.228	0.043	0.000[a] – 0.934
	Canyons, drainages	0.235	0.169	1.391	0.264	0.980 – 1.802
	Gentle hillsides	0.382	0.480	0.796	0.151	0.603 – 0.989
	Steep hillsides	0.176	0.096	1.846	0.351	1.275 – 2.416
	Ridges, hilltops	0.191	0.190	1.005	0.191	0.622 – 1.387
F18	Valley basins, flats	0.002	0.012	0.195	0.043	0.000[a] – 1.324
	Canyons, drainages	0.291	0.181	1.608	0.356	1.343 – 1.873
	Gentle hillsides	0.380	0.443	0.858	0.190	0.718 – 0.998
	Steep hillsides	0.122	0.120	1.014	0.225	0.677 – 1.351
	Ridges, hilltops	0.204	0.243	0.839	0.186	0.619 – 1.059
F19	Valley basins, flats	0.016	0.051	0.308	0.064	0.000[a] – 1.114
	Canyons, drainages	0.254	0.172	1.476	0.308	1.068 – 1.884
	Gentle hillsides	0.409	0.477	0.858	0.179	0.663 – 1.053
	Steep hillsides	0.124	0.114	1.089	0.228	0.572 – 1.607
	Ridges, hilltops	0.197	0.186	1.057	0.221	0.669 – 1.446
F58	Valley basins, flats	0.010	0.013	0.733	0.155	0.000[a] – 2.074
	Canyons, drainages	0.332	0.247	1.344	0.284	1.072 – 1.616
	Gentle hillsides	0.336	0.363	0.925	0.195	0.718 – 1.131
	Steep hillsides	0.147	0.156	0.941	0.198	0.578 – 1.303
	Ridges, hilltops	0.176	0.221	0.797	0.168	0.504 – 1.089
M15a	Valley basins, flats	0.000	0.024	0.000	0.000	0.000[a] – 1.966
	Canyons, drainages	0.392	0.251	1.561	0.394	1.033 – 2.088
	Gentle hillsides	0.354	0.338	1.048	0.264	0.620 – 1.475
	Steep hillsides	0.114	0.147	0.773	0.195	0.038 – 1.508
	Ridges, hilltops	0.139	0.239	0.582	0.147	0.037 – 1.127

[a] Negative lower limit was changed to 0.000.

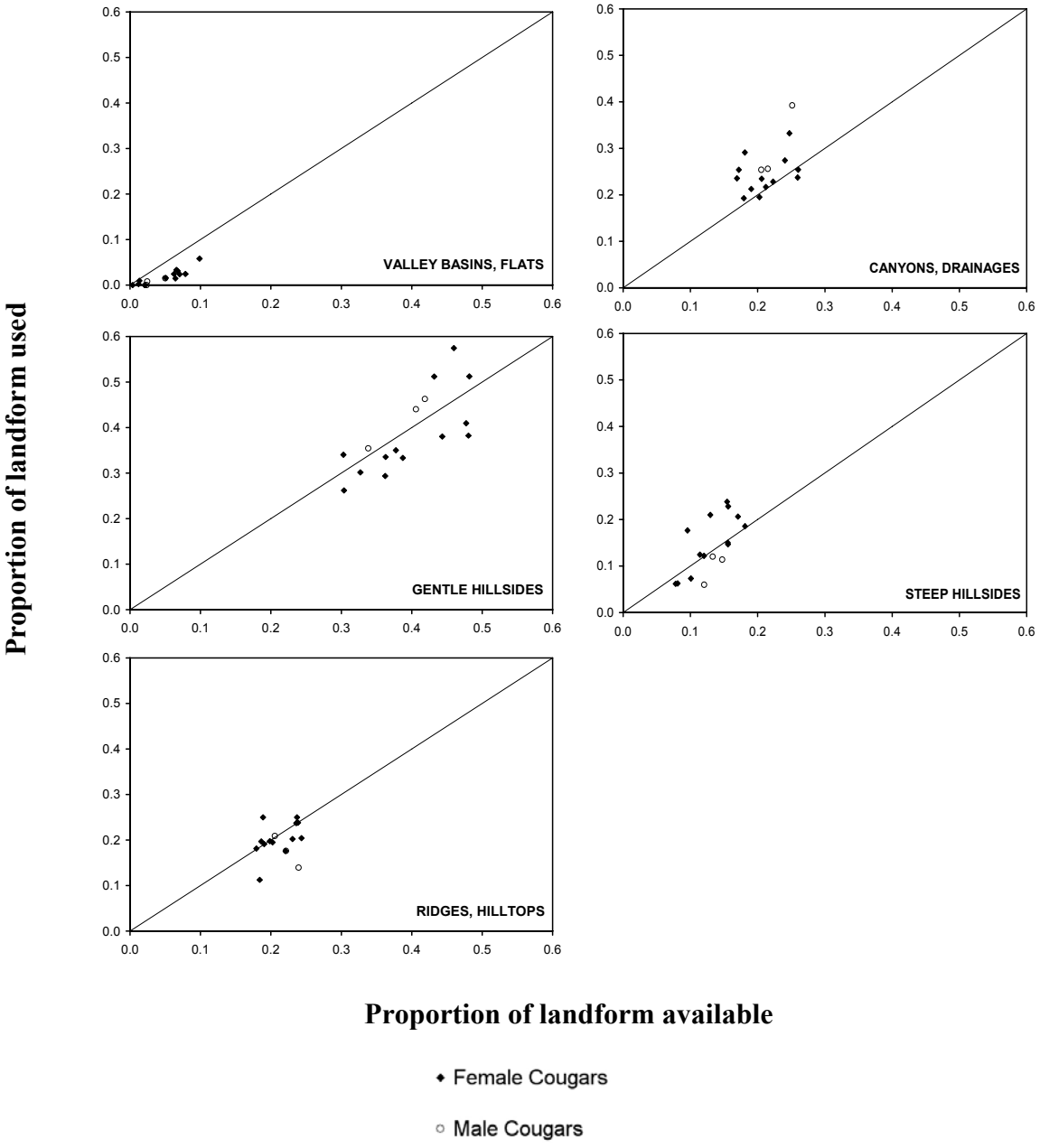

Figure 22. Third-order selection by 3 male and 13 female cougars for 5 landforms on the Oquirrh Mountains, Utah. For each landform, proportional availability was quantified by the individual's 95% fixed kernel home range, and use was quantified by the individual's buffered radiolocations. Line indicates where use and availability would be perfectly equal.

Table 29. Number of radiolocations observed and number expected by landform class in home ranges of 20 female cougars on Monroe Mountain, Utah. Third-order selection was tested at the individual level using chi-square goodness-of-fit tests, and an overall population-level test of selection was conducted by summing the chi-squared statistics and degrees of freedom across all cougars.

Cougar	Valley basins, flats		Canyons, drainages		Gentle hillsides		Steep hillsides		Ridges, hilltops		X^2 Statistic	df	P-value
	Obs[a]	Exp[b]	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp			
F01	2	5	7	5	20	19	5	7	9	7	3.80	4	0.434
F03	2	4	10	8	26	26	8	10	11	9	2.34	4	0.674
F04	3	6	8	6	23	20	4	5	5	6	1.48	4	0.830
F05	3	7	12	12	25	26	15	12	14	12	3.41	4	0.492
F06	3	6	8	6	16	17	5	5	8	6	2.89	4	0.576
F08	2	4	17	12	17	22	15	13	14	14	4.53	4	0.339
F09	0	1	9	8	8	9	6	6	9	8	1.36	4	0.851
F12	3	5	24	21	30	36	17	17	28	23	3.32	4	0.506
F16	1	2	12	10	16	17	9	11	12	10	1.72	4	0.787
F17	1	4	7	5	10	12	6	5	7	5	4.38	4	0.357
F26a	1	2	8	7	7	8	8	8	7	6	0.93	4	0.920
F30	1	1	7	7	8	8	8	8	7	7	0.00	4	1.000
F32b	5	8	7	5	22	23	7	5	6	6	2.77	4	0.597
F35	0	4	10	6	14	16	5	6	10	7	8.37	4	0.079
F36	0	1	9	8	17	18	9	8	9	9	1.31	4	0.860
F40	2	6	8	5	17	17	6	6	7	6	4.63	4	0.331
F43	2	2	7	8	14	11	8	9	7	8	1.18	4	0.881
F49	0	1	10	9	11	12	8	8	10	9	1.31	4	0.860
F52	1	2	7	5	11	11	6	6	5	6	0.97	4	0.914
F53	2	5	8	5	13	17	6	4	7	5	6.34	4	0.175
Population											57.04	76	0.949

[a] Obs = observed

[b] Exp = expected

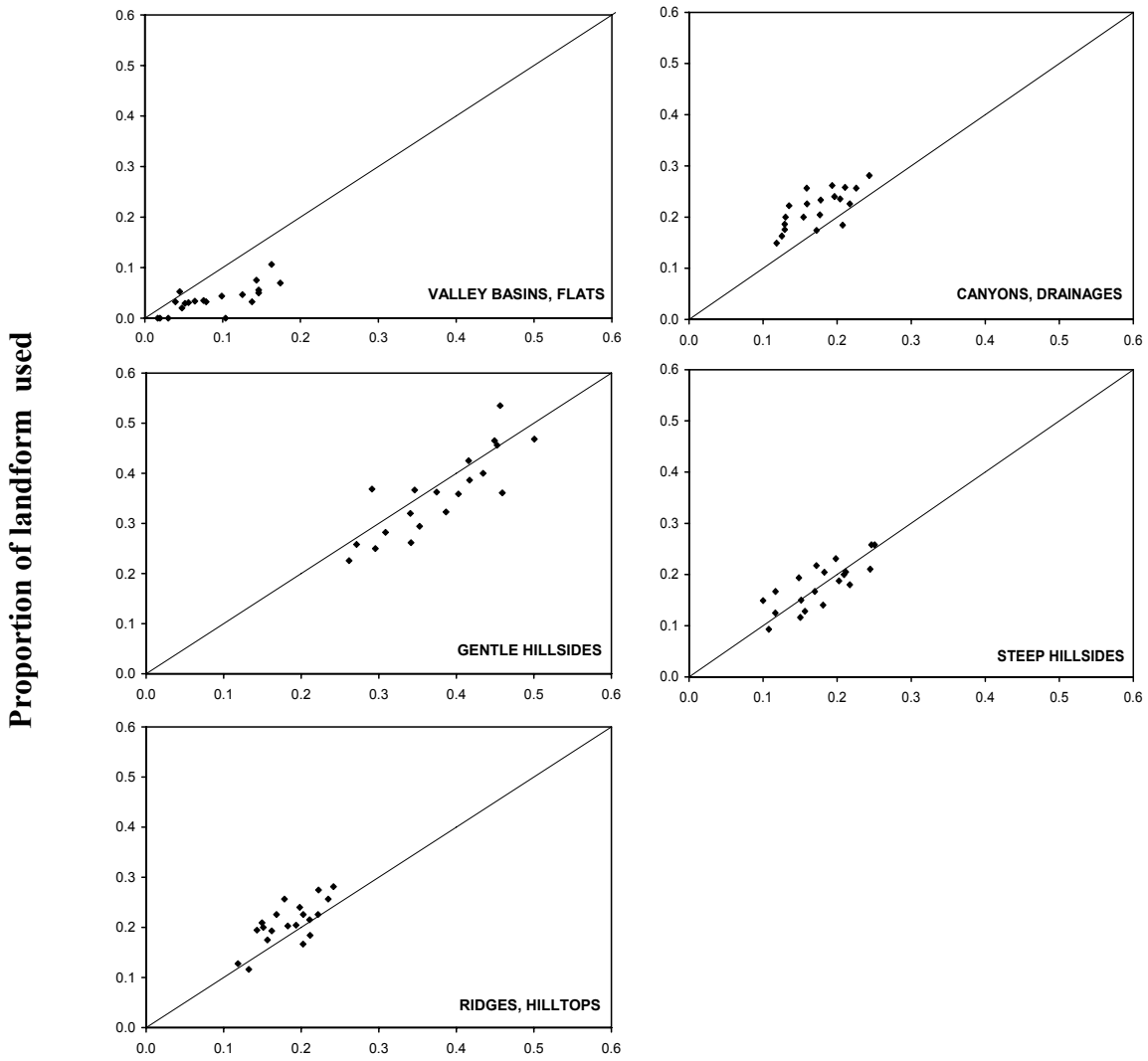

Figure 23. Third-order selection by 20 female cougars for 5 landforms on Monroe Mountain, Utah. For each landform, proportional availability was quantified by the individual's 95% fixed kernel home range, and use was quantified by the individual's buffered radiolocations. Line indicates where use and availability would be equal.

Fine Level: Modeling Selection During Different Behaviors

Model Development. – In total, 349 cache sites, 1,641 daybed sites, and 2,980 nocturnal locations from GPS collar data were used to model cougar resource selection for both scales of availability. Number of locations per cougar ranged from 6 to 116 for cache sites (average = 29 per cougar), from 8 to 357 for daybed sites (average = 137), and from 63 to 727 for nocturnal locations (average = 248).

Multicollinearity diagnostics indicated no explanatory variable was highly collinear with any other explanatory variable. Condition indices were < 10. Therefore, all variables were retained in modeling efforts. AIC_c correction for small sample size was used for the caches dataset because the ratio of number of parameters to sample size was less than 40 (Burnham and Anderson 2002). The datasets for the other behaviors (daybeds and nocturnal activities) were of sufficient size to use AIC.

Of the 20 resource selection models considered for each scale and behavior, the majority were poor approximations to the data because ΔAIC values were greater than 10. There were a few top-ranked models that were plausible based on ΔAIC values ≤ 4. This conclusion was also supported by the Akaike weights (*w*), which in most cases were zero for models that were not in the top-ranked group. For each scale and behavior, there were from 2 to 4 plausible resource selection models. The global (or saturated) models often ranked fairly high among the model sets, which may be an indication that AIC methods were overfitting the data. This further justifies the decision to select the most parsimonious out of the top-ranked models as the "best" model. All variables in the most

parsimonious model were in common with the other top-ranked models. That is, the most parsimonious model was essentially a reduced form of the other top-ranked models.

In the discrete choice models, some pair-wise comparisons of levels of categorical variables may not be meaningful because of the lack of adjacency of some land cover types. For example, given that coniferous forest rarely occurred adjacent to agriculture, these 2 types would not be in the same choice set, and the ability to detect a difference is limited. This was reflected in large upper confidence limit in some of the contrast tests for the fine scale models.

Cougar resource selection varied depending on both behavior and scale. That is, cougars used resources differently for the 3 behaviors examined in this study, and when considering availability of resources in a localized area (also referred to as fine or discrete choice scale) versus across the home range (coarse scale). Across all behaviors and scales, models without land cover as an explanatory variable ranked extremely low to last in all model sets, indicating that this variable had a large effect on resource selection. However, models using only land cover (i.e., single variable models) also ranked low, indicating that there were likely other variables influencing cougar resource selection. The results from the 6 models (3 behaviors x 2 scales) are discussed in further detail below, organized by behavior.

Cache Site Model: Home Range Scale. – Likelihood ratio tests indicated that for cache site selection at the home range scale the global model fit well ($\chi^2 = 234.19$, df = 24, $p < 0.001$). AIC_c values suggested Model 1 as the best and most parsimonious approximating model of cougar cache site selection, given availability of resources in the home range (Table 30). The model included the following 5 variables: aspect, diversity,

Table 30. Model selection results for 20 coarse scale (within home range) models of cougar resource selection for prey caching behavior in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC_c. ΔAIC is the difference in AIC_c units from the highest ranking model. Maximized log-likelihood function ($\log(L)$), number of parameters (K), and model AIC weights (w) are also presented.

Model No.	Model	$\log(L)$	K	AICc	Δ_{AIC}	w
1	**landcov, aspect, diversity, elev, landform**	**-798.91**	**17**	**1,633.68**	**0.00**	**0.265**
2	landcov, aspect, diversity, edge, elev, landform	-797.83	18	1,633.72	0.04	0.259
3	landcov, aspect, diversity, elev, landform, slope	-798.35	18	1,634.76	1.08	0.154
4	landcov, aspect, dist rds, diversity, edge, elev, landform, slope	-797.20	20	1,636.97	3.29	0.051
5	landcov, aspect, dist streams, diversity, elev, slope	-805.88	15	1,643.20	9.52	0.002
6	(GLOBAL) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landcov, landform, slope, slopesq, sdslope	-796.43	24	1,644.57	10.89	0.001
7	landcov, aspect, dist streams, diversity, edge, elev, elevsq	-805.98	16	1,645.60	11.92	0.001
8	landcov, diversity, edge, elev, elevsq, landform, slope	-805.25	17	1,646.35	12.67	0.000
9	landcov, aspect, edge, landform, slope, slopesq	-804.84	18	1,647.75	14.07	0.000
10	landcov, diversity, elev, landform, slope, slopesq	-807.20	16	1,648.05	14.37	0.000
11	landcov, edge, landform, slope	-811.70	14	1,652.67	18.99	0.000
12	landcov, edge, landform	-813.43	13	1,653.95	20.27	0.000
13	landcov, dist rds, edge, landform, slope	-811.68	15	1,654.79	21.11	0.000
14	landcov, landform, slope	-815.26	13	1,657.60	23.92	0.000
15	landcov, dist streams, diversity, elev, elevsq	-816.90	12	1,658.73	25.05	0.000
16	landcov, landform	-817.08	12	1,659.10	25.42	0.000
17	landcov, dist streams, edge, slope, slopesq, sdslope	-822.54	13	1,672.17	38.49	0.000
18	landcov	-829.55	8	1,675.53	41.85	0.000
19	landcov, slope, slopesq, sdslope	-826.81	11	1,676.41	42.73	0.000
20	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-862.51	16	1,758.65	124.97	0.000

elevation, landform, and land cover. There were 3 other top-ranked cache site models with $\Delta AIC \leq 4$ (Model 2, Model 3, and Model 4) (Table 30). Model 2 included the variables listed above plus the edge variable; Model 3 included the variables in the best model plus slope; and the last top-ranked model (Model 4) added edge, slope, and distance to roads.

Coefficients from Model 1 indicated that the areas cougars selected for caching prey, given availability of resources in the home range, were characterized by southern and eastern aspects, a greater diversity of vegetation types, lower elevation, canyon landform, and deciduous vegetation with overstory cover (deciduous woodlands, deciduous forests, and riparian) (Table 31). Odds ratios indicated that the odds of cougar using southern exposures for caching behavior were approximately 2 times greater than the odds of using either northern or western exposures, and 1.4 times the odds of using eastern exposures. Odds of cougar using eastern aspects were 1.4 times greater than the odds of using northern aspects.

The odds of cougar using a site for caching prey at the home range scale increased by 20% for every 1-unit increase in the diversity index (i.e., for every 1 additional land cover type), and by 20% for every 100-m decrease in elevation (Table 31). Average elevation of cache locations was 1,871 m, which was lower than the average for both daybed and nocturnal use locations (1,962 m and 1,909 m, respectively) (Table 32).

Results from contrast tests indicated canyon landforms were more likely to be used for caching prey compared to valleys, hills, and ridges. Ridges were less likely to be used at the home range scale compared to the other landforms. Odds of cougar

Table 31. Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the home range scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.27(asp_N) + 0.09(asp_E) + 0.44(asp_S) +	aspect (asp)	N vs. W	1.00	1.00	0.65 - 1.54	0.990
0.18(div) - 0.002(elev) - 0.85(LC_rock) +		**E vs. N**	**1.43**	**0.70**	**1.03 - 2.00**	**0.049**
0.20(LC_conifF) + 0.90 (LC_decidF) +		E vs. W	1.44	0.69	0.96 - 2.16	0.093
1.01(LC_decidW) - 0.08(LC_conifW) -		**S vs. N**	**2.04**	**0.49**	**1.43 - 2.94**	**0.001**
0.76(LC_shrub) - 1.32(LC_grass) +		**S vs. E**	**1.41**	**0.71**	**1.03 - 1.96**	**0.049**
2.14(LC_ripar) - 0.48(LF_vall) +		**S vs. W**	**2.04**	**0.49**	**1.34 - 3.13**	**0.003**
0.47(LF_cyn) + 0.15(LF_gentleHill) +	diversity (div)		**1.20**	**0.83**	**1.05 - 1.37**	
0.25(LF_steepHill)	elevation (elev) (100-m units)		**0.86**	**1.16**	**0.78 - 0.94**	
	landcover (LC)	rock vs. grass	1.60	0.63	0.18 - 14.02	0.781
		rock vs. disturbed	1.49	0.67	0.15 - 14.52	0.803
		conif. forest vs. rock	2.86	0.35	0.23 - 33.33	0.509
		conif. forest vs. conif. woodl.	1.32	0.76	0.26 - 6.69	0.803
		conif. forest vs. shrub	2.60	0.38	0.54 - 12.57	0.337
		conif. forest vs. grass	4.58	0.22	0.82 - 25.64	0.150
		conif. forest vs. disturbed	4.27	0.23	0.67 - 27.17	0.195
		decid. forest vs. rock	5.88	0.17	0.69 - 50.00	0.173
		decid. forest vs. conif. forest	2.00	0.50	0.41 - 10.00	0.500
		decid. forest vs. conif. woodl.	**2.67**	**0.37**	**1.05 - 6.74**	**0.092**
		decid forest vs. shrub	**5.25**	**0.19**	**2.25 - 12.24**	**<0.001**
		decid. forest vs. grass	**9.24**	**0.11**	**3.10 - 27.5**	**<0.001**
		decid. forest vs. disturbed	**8.61**	**0.12**	**2.36 - 31.43**	**0.004**
		decid. woodl. vs. rock	6.67	0.15	0.85 - 50.00	0.139
		decid. woodl. vs. conif. forest	2.27	0.44	0.50 - 10.00	0.406
		decid. woodl. vs. decid. forest	1.12	0.89	0.53 - 2.33	0.812

Table 31 (continued). Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the home range scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.27(asp_N) + 0.09(asp_E) + 0.44(asp_S) + 0.18(div) - 0.002(elev) - 0.85(LC_rock) + 0.20(LC_conifF) + 0.90 (LC_decidF) + 1.01(LC_decidW) - 0.08(LC_conifW) - 0.76(LC_shrub) - 1.32(LC_grass) + 2.14(LC_ripar) - 0.48(LF_vall) + 0.47(LF_cyn) + 0.15(LF_gentleHill) + 0.25(LF_steepHill)		**decid. woodl. vs. conif. woodl.**	**2.98**	**0.34**	**1.75 - 5.07**	**<0.001**
		decid. woodl. vs. shrub	**5.87**	**0.17**	**3.97 - 8.69**	**<0.001**
		decid. woodl. vs. grass	**10.33**	**0.10**	**4.66 - 22.91**	**<0.001**
		decid. woodl. vs. disturbed	**9.62**	**0.10**	**3.36 - 27.57**	**<0.001**
		conif. woodl. vs. rock	2.17	0.46	0.27 - 16.67	0.563
		conif. woodl. vs. shrub	**1.97**	**0.51**	**1.09 - 3.55**	**0.063**
		conif. woodl. vs. grass	**3.46**	**0.29**	**1.39 - 8.64**	**0.023**
		conif. woodl. vs. disturbed	**3.23**	**0.31**	**1.02 - 10.19**	**0.103**
		shrub vs. rock	1.10	0.91	0.14 - 8.33	0.927
		shrub vs. grass	1.76	0.57	0.77 - 4.04	0.274
		shrub vs. disturbed	1.64	0.61	0.56 - 4.83	0.492
		riparian vs. rock	**20.00**	**0.05**	**1.85 - 213.22**	**0.037**
		riparian vs. conif. forest	7.14	0.14	0.97 - 50.00	0.114
		riparian vs. decid. forest	3.45	0.29	0.81 - 14.29	0.162
		riparian vs. decid. woodl.	3.13	0.32	0.90 - 10.00	0.139
		riparian vs. conif. woodl.	**9.09**	**0.11**	**2.44 - 33.33**	**0.003**
		riparian vs. shrub	**16.67**	**0.06**	**5.26 - 50.00**	**<0.001**
		riparian vs. grass	**33.33**	**0.03**	**7.69 - 100.00**	**<0.001**
		riparian vs. disturbed	**29.65**	**0.03**	**6.21 - 141.60**	**<0.001**
	landform (LF)	disturbed vs. grass	1.08	0.93	0.30 - 3.85	0.927
		canyon vs. valley	**2.56**	**0.39**	**1.12 - 5.88**	**0.063**
		canyon vs. gentle hillside	**1.37**	**0.73**	**1.02 - 1.85**	**0.076**
		canyon vs. steep hillside	1.25	0.80	0.81 - 1.91	0.390
		canyon vs. ridge	**2.35**	**0.43**	**1.48 - 3.76**	**0.003**

Table 31 (continued). Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the home range scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
		gentle hillside vs. valley	1.89	0.53	0.83 - 4.17	0.183
		gentle hillside vs. ridge	**1.72**	**0.58**	**1.10 - 2.69**	**0.061**
		steep hillside vs. valley	2.08	0.48	0.85 - 5.00	0.183
		steep hillside vs. gentle hillside	1.10	0.91	0.73 - 1.67	0.721
		steep hillside vs. ridge	**1.89**	**0.53**	**1.12 - 3.19**	**0.061**
		ridge vs. valley	1.09	0.92	0.44 - 2.70	0.849

Table 32. Average values calculated from cougar GPS data for each continuous explanatory variable used in modeling resource selection in the Oquirrh Mountains, Utah. Minimum and maximum values are given in parentheses.

Behavior	n	Elevation (m)	Slope (%)	SD slope	Dist. roads (m)	Dist. stream (m)	Land cover diversity
Cache	349	**1,871.4** (1,449.2, 2,598.8)	**30.5** (3.7, 73.5)	**9.6** (1.7, 20.3)	**308.2** (0, 2,072.4)	**118.8** (0, 1,925.9)	**2.4** (1, 5)
Daybed	1,641	**1,961.8** (1,478.7, 2,990.0)	**37.8** (2.5, 86.5)	**10.4** (1.9, 24.1)	**415.4** (0, 2,653.8)	**88.8** (0, 2,082.8)	**2.2** (1, 6)
Nocturnal activity	2,980	**1,909.4** (1,306.0, 2,992.8)	**31.8** (0.6, 80.2)	**9.9** (0.7, 27.3)	**308.6** (0, 2,462.2)	**124.9** (0, 2,451.2)	**2.3** (1, 6)

caching in canyons were 2.6, 1.4, and 2.4 times greater than the odds of using these other landforms, respectively (Table 31). However, there was no difference in use of canyons versus steep hills. Odds of caching on ridges decreased by 42% compared to gentle hills, 47% compared to steep hills, and by 57% compared to canyons, but there was no difference in use of ridges compared to valleys.

The odds of cougar using riparian, deciduous woodlands, and deciduous forests for caching at the home range scale were greater than the odds of using more open types, including shrublands, but particularly grasslands and disturbed areas. Odds of caching in riparian were 16.7, 33.3, and 29.7 times greater than the odds of caching in shrublands, grasslands, or disturbed types (Table 31). The odds of using deciduous woodlands were

5.9, 10.3, and 9.6 times greater than odds of using shrublands, grasslands, or disturbed areas, respectively. For deciduous forests, the odds of use were 5.3, 9.2, and 8.6 times greater than the odds of using shrublands, grasslands, or disturbed areas.

Coniferous woodlands were used more frequently than the open types, but less frequently than the deciduous woodlands and deciduous forests. Odds of use of coniferous woodlands were 2 times greater for shrubland, 3.5 times greater compared to grassland, and 30 times greater than disturbed; but odds of using coniferous woodland decreased by 66% compared to deciduous woodlands, 63% compared to deciduous forest, and 89% compared to riparian.

No distinction was apparent among the cover types that were most likely to be used. That is, there was no difference in the odds of using of deciduous woodland, deciduous forest, or riparian types compared to each other. Neither was there a distinction apparent among the open cover types since there was no difference in odds of use among shrub, grass, or disturbed types.

Cougars used coniferous forests in proportion to availability when caching since the odds of use was not greater or less than use of any other type. Cache locations in rocky cover types were rare, and no conclusions could be made about odds of using this cover type relative to other types available in the home range. Agriculture was never used for caching prey, and any random locations located in this type were excluded from the analysis.

Cache Site Model: Discrete Choice Scale.– Likelihood ratio tests indicated that for cache site selection at the discrete choice scale the global model fit well ($\chi^2 = 287.77$, $df = 24$, $p < 0.001$). Models of cache site selection at the discrete choice scale were

similar to selection at the home range scale, but differed by 2 explanatory variables. The use of AIC_c suggested Model 1 as the best and most parsimonious approximating model of cougar cache site selection given availability of resources in a localized area. Model 1 included the following 5 variables: aspect, diversity, edge, landform, and land cover (Table 33). There were 2 other top-ranked cache site models with $\Delta AIC \leq 4$: Model 2, which included the variables listed above plus distance to streams and slope, and Model 3, which, added elevation, elevation^2, and slope.

Similar to home range scale results, cougars selected areas with southern and eastern aspects, a greater diversity of land cover types, canyon landforms, and land cover types with overstory cover (woodlands, forests, and riparian) for caching prey at the discrete choice scale (Table 34). At the discrete choice scale, cougars avoided edge when caching prey, whereas there was no edge effect in the best home-range scale model. In addition, elevation was not included in the best discrete choice model for caching behavior, but was included in the best home range scale model.

Results from contrast tests indicated that the odds of cougar caching prey on southern aspects were approximately 2 times greater than odds of caching on either northern or western aspects. Eastern exposures were also used more than western (odds were 1.7 times greater), but no other distinctions among use of aspects were apparent (Table 34). Odds of using a site for caching prey increased 1.3 times for every 1-unit increase in land cover diversity. Odds of caching prey in non-edge habitat were 1.4 times the odds of caching in edge habitat. In contrast, 70% of cache locations from all cougars

Table 33. Model selection results for 21 fine scale (discrete choice) models of cougar resource selection for prey caching behavior in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC. ΔAIC is the difference in AIC units from the highest ranking model. Maximized log-likelihood function (log(*L*)), number of parameters (*K*), and model AIC weights (*w*) are also shown.

Model No.	Model	log(*L*)	*K*	AICc	Δ_{AIC}	*w*
1	**landcov, aspect, diversity, edge, landform**	**-482.53**	**17**	**1,000.91**	**0.00**	**0.60**
2	landcov, aspect, dist streams, diversity, edge, landform, slope	-481.41	19	1,003.12	2.21	0.20
3	landcov, aspect, diversity, edge, elev, elevsq, landform, slope	-480.87	20	1,004.30	3.39	0.11
4	landcov, aspect, edge, landform	-486.10	16	1,005.85	4.94	0.05
5	landcov, aspect, dist rds, edge, landform	-486.06	17	1,007.97	7.06	0.02
6	landcov, aspect, landform, slope, slopesq	-487.04	17	1,009.93	9.02	0.01
7	landcov, diversity, landform, slope, slopesq	-489.57	15	1,010.59	9.68	0.00
8	(GLOBAL) landcov, aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-480.87	24	1,012.93	12.02	0.00
9	landcov, aspect, dist rds, landform, slope, slopesq, sd slope	-486.90	19	1,014.10	13.19	0.00
10	landcov, landform	-494.46	12	1,013.86	12.95	0.00
11	landcov, edge, landform	-493.71	13	1,014.50	13.59	0.00
12	landcov, landform, slope	-493.80	13	1,014.68	13.77	0.00
13	landcov, edge, landform, slope	-493.07	14	1,015.40	14.49	0.00
14	landcov, landform, slope, slopesq	-493.78	14	1,016.82	15.91	0.00
15	landcov, dist streams, landform, slope, slopesq, sdslope	-493.31	16	1,020.26	19.35	0.00
16	landcov, aspect, dist streams, diversity, edge, elev, elevsq	-497.77	16	1,029.17	28.26	0.00
17	landcov, aspect, diversity, edge	-501.78	13	1,030.65	29.74	0.00
18	landcov, dist streams, edge, slope, slopesq, sdslope	-507.33	13	1,041.75	40.84	0.00
19	landcov, edge	-513.08	9	1,044.69	43.78	0.00
20	landcov	-514.49	8	1,045.39	44.48	0.00
21	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-577.63	16	1,188.90	187.99	0.00

Table 34. Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the discrete choice scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.219(asp_N) + 0.169(asp_E) + 0.425(asp_S) +	aspect (asp)	N vs. W	1.17	0.85	0.68 - 2.00	0.569
0.274(div) - 0.171(edge) - 0.443(LC_rock) +		E vs. N.	1.47	0.68	1.00 - 2.17	0.075
0.887(LC_conifF) + 1.334(LC_decidF) +		**E vs. W**	**1.72**	**0.58**	**1.03 - 2.89**	**0.075**
1.287(LC_decidW) + 0.873(LC_conifW) -		**S. vs. N.**	**1.89**	**0.53**	**1.22 - 2.94**	**0.014**
1.053(LC_shrub) - 1.692(LC_grass) +		S. vs. E	1.30	0.77	0.88 - 1.89	0.229
0.931(LC_ripar) - 0.358(LF_vall) + 0.921(LF_cyn)		**S vs. W**	**2.22**	**0.45**	**1.33 - 3.72**	**0.014**
- 0.077(LF_gentleHill) + 0.132(LF_steepHill)	diversity (div)		**1.32**	**0.76**	**1.08 - 1.61**	
	edge (edge)	**non-edge vs. edge**	**1.41**	**0.71**	**1.02 - 1.92**	
	landcover (LC)	rock vs. shrub	1.84	0.54	0.21 - 16.13	0.697
		rock vs. grass	3.49	0.29	0.34 - 35.74	0.439
		rock vs. disturbed	5.37	0.19	0.44 - 65.04	0.353
		conif. forest vs. rock	3.85	0.26	0.28 - 50.00	0.456
		conif. forest vs. conif. woodl.	1.01	0.99	0.15 - 6.69	0.988
		conif. forest vs. shrub	**6.96**	**0.14**	**1.16 - 41.59**	**0.080**
		conif. forest vs. grass	**13.19**	**0.08**	**1.81 - 95.94**	**0.028**
		conif. forest vs. disturbed	**20.32**	**0.05**	**2.34 - 176.50**	**0.018**
		decid. forest vs. rock	5.88	0.17	0.67 - 50.00	0.222
		decid. forest vs. conif. forest	1.56	0.64	0.29 - 8.33	0.697
		decid. forest vs. decid. woodl.	1.05	0.95	0.42 - 2.60	0.984
		decid. forest vs. conif. woodl.	1.59	0.63	0.49 - 5.14	0.612
		decid forest vs. shrub	**10.87**	**0.09**	**3.97 - 29.75**	**<0.001**
		decid. forest vs. grass	**20.60**	**0.05**	**5.5 - 77.29**	**<0.001**
		decid. forest vs. riparian	1.50	0.67	0.37 - 6.11	0.697
		decid. forest vs. disturbed	**31.75**	**0.03**	**6.53 - 154.30**	**<0.001**

Table 34 (continued). Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the discrete choice scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.219(asp_N) + 0.169(asp_E) + 0.425(asp_S) +		decid. woodl. vs. rock	5.56	0.18	0.67 - 50.00	0.222
0.274(div) - 0.171(edge) - 0.443(LC_rock) +		decid. woodl. vs. conif. forest	1.49	0.67	0.26 - 8.33	0.732
0.887(LC_conifF) + 1.334(LC_decidF) +		decid. woodl. vs. conif. woodl	1.51	0.66	0.72 - 3.19	0.433
1.287(LC_decidW) + 0.873(LC_conifW) -		**decid. woodl. vs. shrub**	**10.38**	**0.10**	**6.47 - 16.66**	**<0.001**
1.053(LC_shrub) - 1.692(LC_grass) +		**decid. woodl. vs. grass**	**19.67**	**0.05**	**7.48 - 51.75**	**<0.001**
0.931(LC_ripar) - 0.358(LF_vall) + 0.921(LF_cyn)		decid. woodl. vs. riparian	1.43	0.70	0.48 - 4.23	0.692
- 0.077(LF_gentleHill) + 0.132(LF_steepHill)		**decid. woodl. vs. disturbed**	**30.31**	**0.03**	**8.21 - 112.00**	**<0.001**
		conif. woodl. vs. rock	3.70	0.27	0.39 - 33.33	0.426
		conif. woodl. vs. shrub	**6.86**	**0.15**	**3.05 - 15.41**	**<0.001**
		conif. woodl. vs. grass	**13.00**	**0.08**	**3.97 - 42.54**	**<0.001**
		conif. woodl. vs. disturbed	**20.02**	**0.05**	**4.56 - 87.87**	**<0.001**
		shrub vs. grass	1.90	0.53	0.71 - 5.05	0.362
		shrub vs. disturbed	2.92	0.34	0.79 - 10.74	0.222
		grass vs. disturbed	1.54	0.65	0.33 - 7.15	0.697
		riparian vs. rock	4.00	0.25	0.36 - 50.00	0.426
	landform (LF)	riparian vs. conif. forest	1.04	0.96	0.14 - 8.33	0.988
		riparian vs. conif. woodl.	1.06	0.94	0.30 - 3.85	0.984
		riparian vs. shrub	**7.14**	**0.14**	**2.44 - 20.00**	**0.001**
		riparian vs. grass	**14.29**	**0.07**	**3.45 - 50.00**	**0.001**
		riparian vs. disturbed	**21.21**	**0.05**	**4.23 - 106.30**	**0.001**
		valley vs. ridge	1.30	0.77	0.40 - 4.23	0.666
		canyon vs. valley	**3.57**	**0.28**	**1.16 - 11.11**	**0.053**
		canyon vs. gentle hillside	**2.71**	**0.37**	**1.85 - 3.98**	**<0.001**
		canyon vs. steep hillside	**2.20**	**0.45**	**1.31 - 3.71**	**0.010**

Table 34 (continued). Parameter estimates converted to odds scale for Model 1: cougar cache site selection at the discrete choice scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
		canyon vs. ridge	**4.66**	**0.21**	**2.61 - 8.32**	**<0.001**
		gentle hillside vs. valley	1.32	0.76	0.45 - 3.85	0.666
		gentle hillside vs. ridge	**1.72**	**0.58**	**1.02 - 2.90**	**0.072**
		steep hillside vs. valley	1.64	0.61	0.51 - 5.26	0.549
		steep hillside vs. gentle hillsid	1.23	0.81	0.72 - 2.08	0.549
		steep hillside vs. ridge	**2.12**	**0.47**	**1.14 - 3.93**	**0.044**

were in edge habitat on average (Table 35). This emphasizes the importance of considering availability of resources, and various scales rather than simple proportions; otherwise such results could be misleading. Cougars only avoided edge at a localized scale.

Given the choices available in a localized area, cougars used canyons more frequently than all other landforms when caching prey, and ridges were used less frequently. The odds of caching prey in canyons were 3.6, 2.7, 2.2, and 4.6 times greater than the odds of caching in valleys, gentle hillsides, steep hillsides, and ridges, respectively (Table 34). Cougars were approximately half as likely to use ridges compared to gentle hillsides and steep hillsides, and odds of use were reduced by 78% for ridges compared to canyons.

Cougar selection patterns for land cover types were similar at the discrete choice scale and the home range scale, although there were larger effect sizes at the discrete choice scale. Odds of cougar caching prey in deciduous woodlands, deciduous forests, coniferous woodlands, and coniferous forests were greater than odds of caching in shrubland, grassland, and disturbed types. Relative use of deciduous woodlands and deciduous forests were similar. The odds of using deciduous woodlands for caching were 10.4, 19.6, and 30.3 times greater than odds of using shrubland, grassland, or disturbed types given the choices available at the discrete choice scale (Table 34). The odds of using deciduous forests were 10.9, 20.6, and 31.7 times greater than odds of using shrublands, grasslands, or disturbed areas. Patterns in use of coniferous woodland and coniferous forests were similar. Odds of use for both these coniferous types were

Table 35. Percent of cougar GPS locations within levels of categorical variables (edge, aspect, landform, and land cover) used in modeling resource selection in the Oquirrh Mountains, Utah. Sample sizes are the same as that reported in Table 32.

EDGE

Behavior	Edge	Non-edge
Cache	69.3	30.7
Daybed	52.4	47.6
Nocturnal activity	67.5	32.5

ASPECT

Behavior	North	East	South	West
Cache	23.8	35.5	28.9	11.8
Daybed	26.5	31.3	24.3	17.9
Nocturnal activity	21.4	32.7	28.7	17.2

LANDFORM

Behavior	Valley	Drainage	Gentle hills	Steep hills	Ridges
Cache	2.3	33.8	43.3	12.0	8.6
Daybed	0.6	31.9	34.7	14.4	18.4
Nocturnal activity	2.4	25.9	42.0	11.8	18.0

LAND COVER

Behavior	Rocky	Conif. forest	Decid. forest	Decid. woodl.	Conif. woodl.	Shrubland	Grassland	Riparian	Agriculture	Disturbed/ developed
Cache	0.3	0.6	3.7	72.2	5.7	11.5	2.3	2.9	0.0	1.2
Daybed	2.1	1.3	3.4	72.2	7.7	10.7	1.3	0.2	0.0	0.4
Nocturnal activity	2.6	1.1	2.6	50.1	6.4	25.4	9.1	0.2	0.2	2.8

approximately 7, 13, and 20 times greater than odds of use of shrubland, grassland, and disturbed types, respectively.

Odds of cougar caching prey in riparian areas were greater than odds of using shrubland, grassland, and disturbed types, but were not greater or less than any odds for any of the other cover types. The rocky cover type was rare in choice sets, and no conclusions could be made about its use compared to other land cover types, except that it was rarely used overall for caching. As stated previously, cougars never cached prey in agricultural areas.

Daybed Model: Home Range Scale.— Likelihood ratio tests indicated that for daybed selection at the home range scale the global model fit well ($\chi^2 = 989.44$, df = 24, $p < 0.001$). The use of AIC suggested Model 3 was the best and most parsimonious approximating model of cougar daybed selection, given availability of resources in the home range. Model 3 included the following 7 variables: distance to roads, distance to streams, elevation, elevation^2, slope, slope^2, and land cover (Table 36). There were 2 other top-ranked models for daybed selection where $\Delta AIC \leq 4$. One of these (Model 1) included the variables listed above, plus landform and SD slope. The other top-ranked model (Model 2) was the global model, which included all variables.

Coefficients from the best home range scale model (Model 3) indicated that the cougar daybed sites were positively associated streams, moderate to high elevations, and moderately steep slopes, but negatively associated with roads (Table 37). Odds of cougars selecting a site for daybed increased by 2% for every 100-meter increase in

Table 36. Model selection results for 22 coarse scale (within home range) models of cougar resource selection for daybed selection in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC. ΔAIC is the difference in AIC units from the highest ranking model. Maximized log-likelihood function (log(L)), number of parameters (K), and model AIC weights (w) are also shown.

Model No.	Model	log(L)	K	AIC	Δ_{AIC}	w
1	landcov, dist streams, dist rds, elev, elevsq, landform, slope, slopesq, sdslope	-3,896.65	19	7,831.29	0.00	0.642
2	(GLOBAL) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landcov, landform, slope, slopesq, sdslope	-3,892.61	24	7,833.22	1.93	0.245
3	**landcov, dist streams, dist rds, elev, elevsq, slope, slopesq**	**-3,903.38**	**14**	**7,834.76**	**3.47**	**0.113**
4	landcov, aspect, dist streams, dist rds, landform, slope, slopesq, sdslope	-3,905.33	20	7,850.66	19.37	0.000
5	landcov, dist streams, landform, slope, slopesq, sdslope	-3,911.35	16	7,854.70	23.41	0.000
6	landcov, dist streams, edge, landform, slope, slopesq, sdslope	-3,910.76	17	7,855.52	24.23	0.000
7	landcov, aspect, dist streams, dist rds, slope, slopesq	-3,913.38	15	7,856.76	25.47	0.000
8	landcov, aspect, dist streams, slope, slopesq	-3,917.38	14	7,862.77	31.48	0.000
9	landcov, dist streams, slope, slopesq	-3,920.49	11	7,862.98	31.69	0.000
10	landcov, aspect, dist rds, dist streams, diversity, elev, edge, landform, slope	-3,914.19	21	7,870.38	39.09	0.000
11	landcov, dist rds, landform, slope, slopesq, sdslope	-3,922.98	16	7,877.95	46.66	0.000
12	landcov, diversity, elev, elevsq, slope, slopesq	-3,929.64	13	7,885.27	53.98	0.000
13	landcov, aspect, dist streams, dist rds, landform	-3,933.58	17	7,901.16	69.87	0.000
14	landcov, diversity, edge, elev, landform, slope	-3,935.68	16	7,903.35	72.06	0.000
15	landcov, elev, elevsq, slope	-3,940.75	11	7,903.50	72.21	0.000
16	landcov, edge, landform, slope	-3,938.48	14	7,904.96	73.67	0.000
17	landcov, aspect, dist streams, edge, landform	-3,939.86	17	7,913.72	82.43	0.000
18	landcov, dist rds, edge, landform	-3,963.83	14	7,955.67	124.38	0.000
19	landcov, landform	-3,973.70	12	7,971.39	140.10	0.000
20	landcov, edge, landform	-3,972.95	13	7,971.89	140.60	0.000
21	landcov	-3,998.60	8	8,013.20	181.91	0.000
22	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-4,418.26	16	8,268.52	437.23	0.000

Table 37. Parameter estimates converted to odds scale for Model 3: cougar daybed selection at the home range scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.002(d_strm) + 0.0002(d_rds) + 0.0009(elev) - 0.000002(elevsq) + 1.044(LC_rock) + 0.063(LC_conifF) + 0.430(LC_decidF) + 0.867(LC_decidW) + 0.516(LC_conifW) - 0.257(LC_shrub) - 1.735(LC_grass) + 0.6571(LC_ripar) + 0.016(slope) - 0.0004(slopesq)	dist to rd (d_rds) (100-m units)		**1.02**	**0.98**	**1.01 - 1.04**	
	dist to stream (d_strm) (100-m units)		**0.82**	**1.22**	**0.78 - 0.87**	
	elevation (100-m units)		**1.09**	**0.92**	**1.05 - 1.14**	
	elevation^2		**0.98**	**1.02**	**0.97 - 0.99**	
	landcover (LC)	**rock vs. conif. forest**	**2.67**	**0.37**	**1.52 - 4.67**	**0.001**
		rock vs. decid. forest	**1.85**	**0.54**	**1.11 - 3.07**	**0.028**
		rock vs. decid. woodl.	1.19	0.84	0.79 - 1.80	0.48
		rock vs. conif. woodl.	**1.70**	**0.59**	**1.07 - 2.68**	**0.035**
		rock vs. shrub	**3.67**	**0.27**	**2.37 - 5.68**	**< 0.001**
		rock vs. grass	**16.10**	**0.06**	**8.87 - 29.22**	**< 0.001**
		rock vs. riparian	1.47	0.68	0.46 - 4.70	0.597
		rock vs. disturbed	**13.84**	**0.07**	**5.57 - 34.37**	**< 0.001**
		conif. forest vs. shrub	1.38	0.72	0.89 - 2.13	0.195
		conif. forest vs. grass	**6.04**	**0.17**	**3.32 - 10.97**	**< 0.001**
		conif. forest vs. disturbed	**5.19**	**0.19**	**2.09 - 12.93**	**0.001**
		decid. forest vs. conif. forest	1.45	0.69	0.88 - 2.38	0.19
		decid forest vs. shrub	**1.99**	**0.50**	**1.38 - 2.87**	**0.001**
		decid. forest vs. grass	**8.71**	**0.11**	**5.04 - 15.06**	**< 0.001**
		decid. forest vs. disturbed	**7.49**	**0.13**	**3.10 - 18.10**	**< 0.001**
		decid. woodl. vs. conif. forest	**2.22**	**0.45**	**1.47 - 3.33**	**< 0.001**
		decid. woodl. vs. decid. forest	**1.54**	**0.65**	**1.11 - 2.17**	**0.016**
		decid. woodl. vs. conif. woodl.	**1.42**	**0.70**	**1.15 - 1.76**	**0.002**
		decid. woodl. vs. shrub	**3.08**	**0.32**	**2.58 - 3.68**	**< 0.001**
		decid. woodl. vs. grass	**13.49**	**0.07**	**8.67 - 20.98**	**< 0.001**

Table 37 (continued). Parameter estimates converted to odds scale for Model 3: cougar daybed selection at the home range scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.002(d_strm) + 0.0002(d_rds) +		decid. woodl. vs. riparian	1.23	0.81	0.42 - 3.66	0.747
0.0009(elev) - 0.000002(elevsq) +		**decid. woodl. vs. disturbed**	**11.60**	**0.09**	**5.09 - 26.40**	**< 0.001**
1.044(LC_rock) + 0.063(LC_conifF) +		conif. woodl. vs. conif. forest	1.56	0.64	0.99 - 2.50	0.077
0.430(LC_decidF) + 0.867(LC_decidW) +		conif. woodl. vs. decid. forest	1.09	0.92	0.74 - 1.61	0.747
0.516(LC_conifW) - 0.257(LC_shrub) -		**conif. woodl. vs. shrub**	**2.17**	**0.46**	**1.68 - 2.79**	**< 0.001**
1.735(LC_grass) + 0.6571(LC_ripar) +		**conif. woodl. vs. grass**	**9.49**	**0.11**	**5.87 - 15.36**	**< 0.001**
0.016(slope) - 0.0004(slopesq)		**conif. woodl. vs. disturbed**	**8.16**	**0.12**	**3.51 - 18.96**	**< 0.001**
		shrub vs. grass	**4.38**	**0.23**	**2.76 - 6.97**	**< 0.001**
		shrub vs. disturbed	**3.77**	**0.27**	**1.64 - 8.67**	**0.003**
		riparian vs. conif. forest	1.82	0.55	0.57 - 5.88	0.393
		riparian vs. decid. forest	1.25	0.80	0.40 - 3.85	0.747
		riparian vs. conif. woodl.	1.15	0.87	0.38 - 3.45	0.801
		riparian vs. shrub	2.50	0.40	0.83 - 7.69	0.141
		riparian vs. grass	**11.11**	**0.09**	**3.45 - 33.33**	**< 0.001**
		riparian vs. disturbed	**9.40**	**0.11**	**2.42 - 36.52**	**0.002**
		disturbed vs. grass	1.16	0.86	0.46 - 2.94	0.772
	slope (10% units)		1.17	0.85	1.11 - 1.22	
	slopesq		**0.96**	**1.04**	**0.95 - 0.98**	

distance from roads, and odds of use increased by 22% for every 100-m decrease in distance from streams. Daybeds were located 415 m from roads on average, which was more than 100 m further than the average distance away for cache and nocturnal use locations (Table 32).

Odds ratios indicated that the odds of cougar using a site as a daybed increased 9% for every 100-m increase in elevation relative to availability within the home range; however, the highest elevations in a home range were less likely to be used as indicated by the negative coefficient on the quadratic term (Table 37). Average elevation of daybed locations was 1,962 m, which was higher than the average for cache and nocturnal use locations (Table 32).

For every 10% increase in slope, odds of use as daybed site increased by 17% (Table 37). The negative coefficient on the slope^2 term indicated that odds of use increased with steeper slopes, but decreased at the steepest slopes in a home range. That is, cougars used steeper slopes within their home range but once the optimum slope was reached, any further increase in steepness did not increase the probability of use. Average percent slope of daybed locations was 37.8%, which was higher than the average for cache and nocturnal locations.

Results from the contrast tests suggest that odds of cougar using rocky areas and deciduous woodlands for daybed sites were greater than odds of use of any other land cover type available in the home range. In contrast, odds of using disturbed and grassland areas were low compared to other cover types available. Odds of using rocky areas were from 1.7 to 16.1 times greater than the odds of using coniferous woodland and grassland, respectively (Table 37). However, there was no distinction between use of

rock and use of deciduous woodland or riparian types. Similarly, odds of using deciduous woodland were from 1.4 to 13.5 times greater than odds of using coniferous woodland and grassland, respectively.

Riparian areas were more likely to be used when compare to grassland or disturbed areas, but there was no preferential use compared to other land cover types. Odds of using other forest and woodland types besides deciduous woodland (coniferous forest, deciduous forest, and coniferous woodland for a daybed site were greater than the odds of using grassland, disturbed, or shrubland types, but, as stated previously, these types were less likely to be used compared to deciduous woodland or rock types. Agricultural areas were never used for daybed sites, and any random locations in agriculture were excluded from analyses.

Daybed Model: Discrete Choice Scale. – Likelihood ratio tests indicated that for daybed selection at the discrete choice scale the global model fit well ($\chi^2 = 575.92$, df = 24, $p < 0.001$). The use of AIC suggested Model 2 was the best and most parsimonious approximating model of daybed selection, given availability of resources in a localized area. Model 2 included the following 6 variables: aspect, distance to roads, edge, slope, and slope^2, and land cover (Table 38). Only 1 other model was considered a top-ranked model (i.e., where $\Delta AIC \leq 4$) for daybed selection at this scale. This model (Model 1) included the variables listed above in addition to distance to streams and standard deviation of slope. Similar to results at the home range scale, the saturated model ranked high overall, but the AIC value for this model was not within 4 AIC units of the top-ranked model.

Table 38. Model selection results for 20 fine scale (discrete choice) models of cougar resource selection for daybed selection in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC. ΔAIC is the difference in AIC units from the highest ranking model. Maximized log-likelihood function (log(L)), number of parameters (K), and model AIC weights (w) are also shown.

Model No.	Model	log(L)	K	AIC	Δ_{AIC}	w
1	landcov, aspect, dist streams, dist rds, edge, slope, slopesq, sdslope	-2,654.32	17	5,342.65	0.00	0.685
2	**landcov, aspect, dist rds, edge, slope, slopesq**	**-2,657.12**	**15**	**5,344.24**	**1.59**	**0.309**
3	(GLOBAL) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landcov, landform, slope, slopesq, sdslope	-2,652.13	24	5,352.27	9.62	0.006
4	landcov, aspect, dist rds, slope, slopesq, sdslope	-2,667.23	15	5,364.46	21.81	0.000
5	landcov, edge, slope, slopesq	-2,671.65	11	5,365.30	22.65	0.000
6	landcov, aspect, diversity, edge, landform	-2,666.12	17	5,366.24	23.59	0.000
7	landcov, edge, landform, slope, slopesq, sdslope	-2,668.31	16	5,368.62	25.97	0.000
8	landcov, dist rds, slope, slopesq	-2,675.96	11	5,373.93	31.28	0.000
9	landcov, aspect, slope, slopesq, sdslope	-2,673.18	14	5,374.36	31.71	0.000
10	landcov, edge	-2,678.28	9	5,374.56	31.91	0.000
11	landcov, aspect, dist rds, landform, slope	-2,670.90	17	5,375.81	33.16	0.000
12	landcov, aspect, dist streams, slope	-2,677.35	13	5,380.69	38.04	0.000
13	landcov, dist streams, slope, slopesq	-2,679.57	11	5,381.13	38.48	0.000
14	landcov, elev, slope, slopesq	-2,682.16	11	5,386.31	43.66	0.000
15	landcov, landform, slope, slopesq, sdslope	-2,678.23	15	5,386.46	43.81	0.000
16	landcov, aspect, elev, landform	-2,677.32	16	5,386.65	44.00	0.000
17	landcov, dist streams, elev, elevsq, slope	-2,683.96	12	5,391.92	49.27	0.000
18	landcov	-2,688.42	8	5,392.85	50.20	0.000
19	landcov, landform	-2,685.24	12	5,394.48	51.83	0.000
20	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-2,878.54	16	5,789.07	446.42	0.000

Coefficients from the best discrete choice scale model (Model 2) indicated that the areas cougars selected for daybed sites were negatively associated with roads and edge and positively associated with moderate slopes (Table 39). Odds of use were 14% greater for every 100-m increase in distance from roads. Cougars were 25% less likely to use edge compared to non-edge at the discrete choice scale.

Slope effects were less pronounced at the discrete choice scale than at the home range scale, likely due to the limited ability to detect variation across the small extent used to define the choice sets at this scale. There was evidence that cougars selected gentler slopes based on the negative coefficient on the slope term; however, the confidence interval around the odds ratio for slope included 1, indicating there was not a strong linear trend (Table 39). The odds ratio for the quadratic slope term indicated cougars were selecting moderate slopes at the discrete choice scale.

Results from contrast tests on aspect categories suggest that odds of using southern aspects were from 22% to 52% greater than odds of using eastern or western aspects. Odds of using northern and eastern aspects for daybeds were 28% and 20% more likely than odds of using western aspects, respectively (Table 39).

Results from contrast tests on land cover types indicated that cougar preferred rocky, deciduous woodland, and riparian types over all other types when selecting a daybed sites at the discrete choice scale. However, use of these 3 types relative to each other could not be distinguished. Shrubland, grassland, and disturbed types were avoided compared to other cover types. Odds of using rock types were from 1.8 (coniferous woodland) to 18.7 (grassland) times greater than odds of using other land cover types for daybed sites (Table 39). Odds of cougar using deciduous woodlands for a daybed site were from 1.6

Table 39. Parameter estimates converted to odds scale for Model 2: cougar daybed selection at the discrete choice scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
0.034(asp_N) - 0.004(asp_E) +	aspect (asp)	N vs. E	1.04	0.96	0.88 - 1.23	0.661
0.193(asp_S) - 0.149(edge) + 0.001(d_rds)		**N vs. W**	**1.29**	**0.78**	**1.04 - 1.60**	**0.056**
+ 1.030(LC_rock) + 0.308(LC_conifF) +		S vs. N	1.18	0.85	0.95 - 1.43	0.153
0.331(LC_decidF) + 0.892(LC_decidW) +		**S vs E**	**1.22**	**0.82**	**1.02 - 1.45**	**0.058**
0.419(LC_conifW) - 0.599(LC_shrub) -		**E vs. W**	**1.25**	**0.80**	**1.01 - 1.53**	**0.058**
1.898(LC_grass) + 1.251(LC_ripar) -		**S vs. W**	**1.52**	**0.66**	**1.24 - 1.86**	**< 0.001**
0.003(slope) - 0.0004(slopesq)	dist to rd (d_rds) (100-m units)		**1.14**	**0.88**	**1.06 - 1.22**	
	edge	**non-edge vs. edge**	**1.35**	**0.74**	**1.19 - 1.52**	
	landcover (LC)	**rock vs. conif. forest**	**2.06**	**0.49**	**1.10 - 3.87**	**0.036**
		rock vs. decid. forest	**2.01**	**0.50**	**1.16 - 3.49**	**0.021**
		rock vs. decid. woodl.	1.15	0.87	0.75 - 1.77	0.637
		rock vs. conif. woodl.	**1.84**	**0.54**	**1.11 - 3.06**	**0.029**
		rock vs. shrub	**5.10**	**0.20**	**3.22 - 8.08**	**< 0.001**
		rock vs. grass	**18.69**	**0.05**	**9.56 - 36.52**	**< 0.001**
		rock vs. disturbed	**15.88**	**0.06**	**5.45 - 46.26**	**< 0.001**
		conif. forest vs. shrub	**2.48**	**0.40**	**1.47 - 4.17**	**0.001**
		conif. forest vs. grass	**9.07**	**0.11**	**4.43 - 18.58**	**< 0.001**
		conif. forest vs. disturbed	**7.71**	**0.13**	**2.55 - 23.35**	**0.001**
		decid. forest vs. conif. forest	1.02	0.98	0.59 - 1.79	0.934
		decid forest vs. shrub	**2.54**	**0.39**	**1.69 - 3.80**	**< 0.001**
		decid. forest vs. grass	**9.29**	**0.11**	**4.92 - 17.55**	**< 0.001**
		decid. forest vs. disturbed	**7.90**	**0.13**	**2.73 - 22.86**	**< 0.001**
		decid. woodl. vs. conif. forest	**1.79**	**0.56**	**1.10 - 2.94**	**0.030**
		decid. woodl. vs. decid. forest	**1.75**	**0.57**	**1.20 - 2.56**	**0.006**

Table 39 (continued). Parameter estimates converted to odds scale for Model 2: cougar daybed selection at the discrete choice scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
0.034(asp_N) - 0.004(asp_E) +		**decid. woodl. vs. conif. woodl.**	**1.60**	**0.63**	**1.20 - 2.15**	**0.003**
0.193(asp_S) - 0.149(edge) + 0.001(d_rds)		**decid. woodl. vs. shrub**	**4.44**	**0.23**	**3.66 - 5.38**	**< 0.001**
+ 1.030(LC_rock) + 0.308(LC_conifF) +		**decid. woodl. vs. grass**	**16.27**	**0.06**	**9.65 - 27.44**	**< 0.001**
0.331(LC_decidF) + 0.892(LC_decidW) +		**decid. woodl. vs. disturbed**	**13.83**	**0.07**	**5.07 - 37.70**	**< 0.001**
0.419(LC_conifW) - 0.599(LC_shrub) -		conif. woodl. vs. conif. forest	1.12	0.89	0.63 - 1.96	0.778
1.898(LC_grass) + 1.251(LC_ripar) -		conif. woodl. vs. decid. forest	1.09	0.92	0.68 - 1.75	0.778
0.003(slope) - 0.0004(slopesq)		**conif. woodl. vs. shrub**	**2.77**	**0.36**	**2.01 - 3.81**	**< 0.001**
		conif. woodl. vs. grass	**10.14**	**0.10**	**5.63 - 18.25**	**< 0.001**
		conif. woodl. vs. disturbed	**8.62**	**0.12**	**3.05 - 24.33**	**< 0.001**
		shrub vs. grass	**3.66**	**0.27**	**2.14 - 6.27**	**< 0.001**
		shrub vs. disturbed	**3.11**	**0.32**	**1.14 - 8.51**	**0.037**
		riparian vs. rock	1.25	0.80	0.35 - 4.55	0.778
		riparian vs. conif. forest	2.56	0.39	0.70 - 9.10	0.198
		riparian vs. decid. forest	2.50	0.40	0.71 - 9.10	0.198
		riparian vs. decid. woodl.	1.43	0.70	0.43 - 4.76	0.650
		riparian vs. conif. woodl.	2.27	0.44	0.67 - 7.70	0.234
		riparian vs. shrub	**6.25**	**0.16**	**1.89 - 20.00**	**0.005**
		riparian vs. grass	**25.00**	**0.04**	**6.25 - 100.00**	**< 0.001**
		riparian vs. disturbed	**19.81**	**0.05**	**4.17 - 94.01**	**< 0.001**
		disturbed vs. grass	1.18	0.85	0.39 - 3.57	0.795
	slope (10% units)		0.97	1.03	0.92 - 1.02	
	slopesq		**0.96**	**1.04**	**0.94 - 0.99**	

(coniferous woodland) to 16.3 (grassland) greater than odds of using other cover types. Odds of using deciduous forest, coniferous forest, and coniferous woodland were only greater than odds of using more open cover types, ranging from 2.5 to 10 times greater than the odds of using shrubland, grassland, and disturbed types. As stated previously, agricultural areas were never used for daybed sites.

Nocturnal Model: Home Range Scale. – Likelihood ratio tests indicated that for nocturnal use at the discrete choice scale the global model fit well ($\chi^2 = 494.54$ df = 24, $p < 0.001$). The use of AIC suggested Model 3 was the best and most parsimonious approximating model of nocturnal resource selection, given availability of resources in the home range. Model 3 included the following 6 variables: aspect, distance to streams, distance to roads, edge, land cover, and landform (Table 40). Two other models were top ranked based on AIC: Model 1, which included the variables above plus diversity and elevation, and Model 2, which was the saturated (or global) model.

Coefficients from the best home range scale model (Model 3) indicated that areas used by cougars during nocturnal hours were more positively associated with edge habitat, streams, and roads (Table 41). Specifically, odds of use were 1.9 times greater for edge compared to non-edge features. Odds of use increased by 4% for every 100-m decrease in distance from streams, and by 3% for every 100-m decrease in distance from roads. In addition, results from contrast tests indicated that cougars were less likely to use northern aspects during nocturnal activities, but more likely to use rock and deciduous woodland cover types, and canyon landforms. Further details on results of contrast tests are given below. Cougars selected east, south, and west aspects to north

Table 40. Model selection results for 20 coarse scale (within home range) models of cougar resource selection during nocturnal activities in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC. ΔAIC is the difference in AIC units from the highest ranking model. Maximized log-likelihood function (log(L)), number of parameters (K), and model AIC weights (w) are also shown.

Model No.	Model	log(L)	K	AIC	Δ_{AIC}	w
1	landcov, aspect, dist streams, diversity, dist rds, edge, elev, landform, sl	-6416.25	22	12876.50	0.00	0.360
2	(GLOBAL) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landcov, landform, slope, slopesq, sdslope	-6413.26	24	12876.53	0.03	0.355
3	**landcov, aspect, dist streams, dist rds, edge, landform**	**-6419.49**	**19**	**12876.97**	**0.47**	**0.285**
4	landcov, aspect, dist streams, edge, landform	-6427.79	18	12891.57	15.07	0.000
5	landcov, aspect, edge, elev, landform, slope, slopesq, sdslope	-6425.34	21	12892.68	16.18	0.000
6	landcov, edge, landform, slope	-6435.51	15	12901.02	24.52	0.000
7	landcov, dist streams, diversity, edge, landform	-6434.68	16	12901.36	24.86	0.000
8	landcov, edge, landform, slope, slopesq, sdslope	-6433.71	17	12901.42	24.92	0.000
9	landcov, edge, elev, landform, slope, slopesq, sdslope	-6432.75	18	12901.51	25.01	0.000
10	landcov, dist streams, diversity, edge, elev, elevsq, landform	-6433.47	18	12902.95	26.45	0.000
11	landcov, dist streams, diversity, edge, elev, landform	-6434.68	17	12903.35	26.85	0.000
12	landcov, edge, landform	-6437.71	14	12903.42	26.92	0.000
13	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-6439.76	16	12911.51	35.01	0.000
14	landcov, dist streams, diversity, edge	-6449.80	12	12923.61	47.11	0.000
15	landcov, aspect, dist streams, elev, landform	-6526.50	18	13089.00	212.50	0.000
16	landcov, dist streams, elev, landform, slope	-6533.07	16	13098.14	221.64	0.000
17	landcov, landform, slope	-6545.35	14	13118.70	242.20	0.000
18	landcov, landform	-6547.36	13	13120.73	244.23	0.000
19	landcov, elev, slope, slopesq, sdslope	-6572.35	13	13170.69	294.19	0.000
20	landcov	-6583.02	9	13184.04	307.54	0.000

Table 41. Parameter estimates converted to odds scale for Model 3: cougar nocturnal resource selection at the home range scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.138(asp_N) - 0.010(asp_E) +	aspect (asp)	**E vs. N**	**1.14**	**0.88**	**1.01 - 1.28**	**0.064**
0.071(asp_S) - 0.0004(dist_strm) -		**S vs. N**	**1.23**	**0.81**	**1.09 - 1.39**	**0.006**
0.0003(dist rds) + 0.324(edge) +		S vs. E	1.09	0.92	0.97 - 1.20	0.224
0.803(LC_rock) - 0.134(LC_conifF) +		**W vs. N**	**1.23**	**0.81**	**1.08 - 1.43**	**0.007**
0.176(LC_decidF) + 0.308(LC_decidW) -		W vs. E	1.09	0.92	0.96 - 1.23	0.224
0.036(LC_conifW) + 0.150(LC_shrub) +		W vs. S	1.01	0.99	0.88 - 1.15	0.921
0.015(LC_grass) - 0.464(LC_ripar)-	dist to stream (d_strm) (100-m units)		**0.96**	**1.04**	**0.93 - 0.99**	
0.660(LC_ag) - 0.339(LF_vall) +	dist to roads (dist rds) (100-m units)		**0.97**	**1.03**	**0.96 - 0.99**	
0.301(LF_cyn) + 0.043(LF_gentleHill) +	edge	**edge vs. non-edge**	**1.91**	**0.52**	**1.75 - 2.10**	
0.040(LF_steepHill)	landcover (LC)	**rock vs. conif. forest**	**2.55**	**0.39**	**1.56 - 4.17**	**0.001**
		rock vs. decid. forest	**1.87**	**0.53**	**1.23 - 2.84**	**0.014**
		rock vs. decid. woodl.	**1.64**	**0.61**	**1.21 - 2.22**	**0.007**
		rock vs. conif. woodl.	**2.31**	**0.43**	**1.64 - 3.26**	**<0.001**
		rock vs. shrub	**1.92**	**0.52**	**1.41 - 2.62**	**<0.001**
		rock vs. grass	**2.20**	**0.45**	**1.59 - 3.05**	**<0.001**
		rock vs. riparian	**3.55**	**0.28**	**1.44 - 8.73**	**0.020**
		rock vs. agric	**4.32**	**0.23**	**1.61 - 11.59**	**0.015**
		rock vs. disturbed	**2.61**	**0.38**	**1.78 - 3.84**	**<0.001**
		conif. forest vs. riparian	1.39	0.72	0.55 - 3.55	0.559
		conif. forest vs. agric	1.69	0.59	0.61 - 4.70	0.425
		conif. forest vs. disturbed	1.03	0.97	0.65 - 1.63	0.917
		decid. forest vs. conif. forest	1.37	0.73	0.85 - 2.22	0.329
		decid. forest vs. conif. woodl.	1.24	0.81	0.88 - 1.74	0.346
		decid forest vs. shrub	1.03	0.97	0.75 - 1.40	0.888

Table 41 (continued). Parameter estimates converted to odds scale for Model 3: cougar nocturnal resource selection at the home range scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.138(asp_N) - 0.010(asp_E) +		decid. forest vs. grass	1.18	0.85	0.85 - 1.63	0.426
0.071(asp_S) - 0.0004(dist_strm) -		decid. forest vs. riparian	1.90	0.53	0.77 - 4.65	0.293
0.0003(dist rds) + 0.324(edge) +		decid. forest vs. agric	2.31	0.43	0.86 - 6.18	0.206
0.803(LC_rock) - 0.134(LC_conifF) +		decid. forest vs. disturbed	1.40	0.71	0.95 - 2.05	0.205
0.176(LC_decidF) + 0.308(LC_decidW) -		**decid. woodl. vs. conif. forest**	**1.56**	**0.64**	**1.04 - 2.33**	**0.089**
0.036(LC_conifW) + 0.150(LC_shrub) +		decid. woodl. vs. decid. forest	1.14	0.88	0.85 - 1.54	0.483
0.015(LC_grass) - 0.464(LC_ripar)-		**decid. woodl. vs. conif. woodl.**	**1.41**	**0.71**	**1.18 - 1.69**	**0.001**
0.660(LC_ag) - 0.339(LF_vall) +		**decid. woodl. vs. shrub**	**1.17**	**0.85**	**1.05 - 1.31**	**0.017**
0.301(LF_cyn) + 0.043(LF_gentleHill) +		**decid. woodl. vs. grass**	**1.34**	**0.75**	**1.15 - 1.56**	**0.001**
0.040(LF_steepHill)		decid. woodl. vs. riparian	2.17	0.46	0.93 - 5.06	0.186
		decid. woodl. vs. agric	**2.63**	**0.38**	**1.03 - 6.77**	**0.125**
		decid. woodl. vs. disturbed	**1.59**	**0.63**	**1.23 - 2.06**	**0.002**
		conif. woodl. vs. conif. forest	1.10	0.91	0.71 - 1.69	0.706
		conif. woodl. vs. riparian	1.53	0.65	0.65 - 3.64	0.426
		conif. wood. vs. agric	1.87	0.53	0.72 - 4.85	0.329
		conif. woodl. vs. disturbed	1.13	0.88	0.84 - 1.53	0.520
		shrub vs. conif. forest	1.33	0.75	0.88 - 2.00	0.293
		shrub vs. conif. woodl.	1.20	0.83	1.00 - 1.45	0.128
		shrub vs. grass	1.14	0.88	0.97 - 1.35	0.215
		shrub vs. riparian	1.85	0.54	0.79 - 4.34	0.293
		shrub vs. agric	2.25	0.44	0.88 - 5.75	0.205
		shrub vs. disturbed	**1.36**	**0.74**	**1.05 - 1.77**	**0.064**
		grass vs. conif. forest	1.16	0.86	0.76 - 1.75	0.559
		grass vs. conif. woodl	1.05	0.95	0.85 - 1.32	0.706

Table 41 (continued). Parameter estimates converted to odds scale for Model 3: cougar nocturnal resource selection at the home range scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
-0.138(asp_N) - 0.010(asp_E) +		grass vs. riparian	1.61	0.62	0.68 - 3.82	0.399
0.071(asp_S) - 0.0004(dist_strm) -		grass vs. agric	1.96	0.51	0.76 - 5.07	0.293
0.0003(dist rds) + 0.324(edge) +		grass vs. disturbed	1.19	0.84	0.89 - 1.58	0.351
0.803(LC_rock) - 0.134(LC_conifF) +		riparian vs. agric	1.22	0.82	0.34 - 4.31	0.797
0.176(LC_decidF) + 0.308(LC_decidW) -		disturbed vs. riparian	1.35	0.74	0.56 - 3.33	0.559
0.036(LC_conifW) + 0.150(LC_shrub) +		disturbed vs. agric.	1.64	0.61	0.63 - 4.35	0.425
0.015(LC_grass) - 0.464(LC_ripar)-	landform (LF)	**canyon vs. valley**	**1.89**	**0.53**	**1.39 - 2.56**	**<0.001**
0.660(LC_ag) - 0.339(LF_vall) +		**canyon vs. gentle hillside**	**1.29**	**0.78**	**1.15 - 1.46**	**<0.001**
0.301(LF_cyn) + 0.043(LF_gentleHill) +		**canyon vs. steep hillside**	**1.30**	**0.77**	**1.11 - 1.52**	**0.003**
0.040(LF_steepHill)		**canyon vs. ridge**	**1.41**	**0.71**	**1.22 - 1.64**	**<0.001**
		gentle hillside vs. valley	**1.47**	**0.68**	**1.10 - 1.96**	**0.017**
		gentle vs. steep hillside	1.00	1.00	0.87 - 1.15	0.970
		gentle hillside vs. ridge	1.09	0.92	0.97 - 1.23	0.198
		steep hillside vs. valley	**1.47**	**0.68**	**1.08 - 2.00**	**0.027**
		steep hillside vs. ridge	1.08	0.93	0.93 - 1.28	0.338
		ridge vs. valley	1.33	0.75	1.00 - 1.79	0.068

aspects during nocturnal activities. Odds of using east, south, and west aspects were 14% to 23% times greater than odds of using north aspects.

Odds of cougar using rocky cover types during nocturnal hours were greater than any other land cover type. Odds of using rocky areas were from 1.6 to 1.9 times greater than the odds of using deciduous woodland, deciduous forest, and agriculture (Table 41). Odds of using rock were from 2.3 to 2.6 times greater than odds of using grassland, coniferous woodland, disturbed, and coniferous forest. Odds of using rock were 3.6 to 4.3 times greater than odds of using riparian and agriculture types, respectively.

Deciduous woodlands were preferred over all other land cover types except rock and riparian during nocturnal activities. Odds of using deciduous woodlands were from 1.2 to 1.6 times greater than odds of using shrubland, grassland, coniferous woodland, coniferous forest, or disturbed, and 2.6 times greater than odds of using agriculture (Table 41). Odds of using deciduous woodland could not be distinguished from odds of using riparian. There was little evidence that open areas (i.e., no overstory cover) were avoided during nocturnal hours. Approximately 50% of cougar nocturnal locations were within deciduous woodlands, whereas 72% of cache and daybed locations were located in deciduous woodlands (Table 35). Among the more open cover types, odds of using shrublands were 40% greater than odds of using disturbed areas.

At the home range scale, cougars preferred canyons but avoided flat landforms during their nocturnal activities. Odds of cougar using canyons during nocturnal activities were 1.3 to 1.4 times greater than odds of using gentle hillsides, steep hillsides, and ridges (Table 41). Odds of using valleys were 53% to 25% less than odds of using canyons, gentle slopes, steep slopes, and ridges.

Nocturnal Model: Discrete Choice Scale. – Likelihood ratio tests indicated that for nocturnal use at the discrete choice scale the global model fit well ($\chi^2 = 202.08$ df = 24, $p < 0.001$). The use of AIC suggested Model 2 was the best and most parsimonious approximating model of resource use during nocturnal hours, given availability of resources in a localized area. Model 2 included the following 4 variables: distance to streams, edge, slope, and land cover (Table 42). Model 1 was the only other model that was top-ranked using AIC, and it included the variables in Model 2 plus aspect.

Only 4 variables explained cougar nocturnal resource use, indicating that cougars may be least selective of resources during nocturnal activities (compared to other behaviors) and when making choices at a localized scale (versus across the entire home range). Results were similar to results at the home range scale, except fewer variables explained nocturnal use. Slope was included in discrete choice model of nocturnal resource selection, but was not included in models considering availability throughout the home range.

Effect sizes for a number of variables were greater at the discrete choice compared to the home range scale. Odds of nocturnal use were 29% greater for edge compared to non-edge areas (Table 43). For every 100-m decrease in distance from streams, odds of cougar use for nocturnal activities increased by 20%. Cougars used gentler slopes relative to availability in a localized area. For every 10% decrease in slope, the odds of cougar using the site increase by 6%.

Similar to results for the home range scale model, cougar used rocky types more than other land cover type during nocturnal activities. Odds of cougar using of rocky areas were from 2.5 to 2.9 greater than the odds of using coniferous woodland, deciduous

Table 42. Model selection results for 20 fine scale (discrete choice) models of cougar resource selection during nocturnal activities in the Oquirrh Mountains, Utah. Models are ordered by ΔAIC. ΔAIC is the difference in AIC units from the highest ranking model. Maximized log-likelihood function (log(*L*)), number of parameters (*K*), and model AIC weights (*w*) are also shown.

Model No.	Model	log(*L*)	*K*	AIC	Δ_{AIC}	*w*
1	landcov, aspect, dist streams, edge, slope	-3,975.37	15	7,980.75	0.00	0.693
2	**landcov, dist streams, edge, slope**	**-3,979.42**	**12**	**7,982.84**	**2.09**	**0.244**
3	landcov, dist streams, diversity, edge, elev, slope	-3,979.32	14	7,986.64	5.89	0.036
4	(GLOBAL) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landcov, landform, slope, slopesq, sdslope	-3,970.74	24	7,989.48	8.73	0.009
5	landcov, aspect, edge, landform, slope	-3,977.06	18	7,990.12	9.37	0.006
6	landcov, dist streams, diversity, edge	-3,983.78	12	7,991.57	10.82	0.003
7	landcov, dist rds, edge, landform, slope	-3,979.95	16	7,991.89	11.14	0.003
8	landcov, aspect, diversity, edge, landform, slope	-3,977.04	19	7,992.08	11.33	0.002
9	landcov, edge, landform, slope, slopesq	-3,980.46	16	7,992.93	12.18	0.002
10	landcov, diversity, landform, slope	-3,980.71	16	7,993.42	12.67	0.001
11	landcov, edge, landform	-3,982.85	14	7,993.70	12.95	0.001
12	landcov, dist streams, slope	-3,992.72	11	8,007.45	26.70	0.000
13	landcov, dist streams, slope, slopesq	-3,992.21	12	8,008.41	27.66	0.000
14	landcov, edge	-3,994.74	10	8,009.48	28.73	0.000
15	landcov, dist streams, dist rds, slope, slopesq, sdslope	-3,991.06	14	8,010.12	29.37	0.000
16	landcov, landform, slope, slopesq, sdslope	-3,993.67	16	8,019.34	38.59	0.000
17	landcov, landform	-3,996.82	13	8,019.65	38.90	0.000
18	landcov, elev, slope, slopesq	-4,001.41	12	8,026.81	46.06	0.000
19	landcov	-4,008.07	9	8,034.14	53.39	0.000
20	(GLOBAL - LC) aspect, dist streams, dist rds, diversity, edge, elev, elevsq, landform, slope, slopesq, sdslope	-4,028.34	15	8,086.68	105.93	0.000

Table 43. Parameter estimates converted to odds scale for Model 2: cougar nocturnal resource selection at the discrete choice scale in the Oquirrh Mountains, Utah. Ninety-five percent confidence intervals (CI) and results of contrast tests on categorical variables are also shown with p-values corrected for multiple comparisons using False Discovery Rate (FDR) methods. Bold font indicates CI on the odds ratio did not include the value 1.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
0.128(edge) - 0.002(d_strm) + 1.308(LC_rock) + 0.042(LC_conifF) + 0.247(LC_decidF) + 0.335(LC_decidW) + 0.376(LC_conifW) + 0.018(LC_shrub) - 0.154(LC_grass) + 0.253(LC_ripar) - 2.16(LC_ag) - 0.006(slope)	dist to stream (d_strm) (100-m units)		**0.84**	**1.19**	**0.78 - 0.90**	
	edge	**edge vs. non-edge**	**1.29**	**0.78**	**1.17 - 1.42**	
	landcover (LC)	**rock vs. conif. forest**	**3.54**	**0.28**	**2.02 - 6.22**	**<0.001**
		rock vs. decid. forest	**2.89**	**0.35**	**1.76 - 4.74**	**<0.001**
		rock vs. decid. woodl.	**2.65**	**0.38**	**1.86 - 3.77**	**<0.001**
		rock vs. conif. woodl.	**2.54**	**0.39**	**1.66 - 3.89**	**<0.001**
		rock vs. shrub	**3.63**	**0.28**	**2.53 - 5.21**	**<0.001**
		rock vs. grass	**4.32**	**0.23**	**2.95 - 6.32**	**<0.001**
		rock vs. riparian	**2.87**	**0.35**	**1.01 - 8.18**	**0.086**
		rock vs. agric	**32.01**	**0.03**	**6.71 - 152.60**	**<0.001**
		rock vs. disturbed	**4.83**	**0.21**	**3.10 - 7.52**	**<0.001**
		conif. forest vs. shrub	1.03	0.97	0.65 - 1.62	0.935
		conif. forest vs. grass	1.22	0.82	0.76 - 1.96	0.559
		conif. forest vs. agric	**9.03**	**0.11**	**1.85 - 44.09**	**0.015**
		conif. forest vs. disturbed	1.36	0.74	0.81 - 2.29	0.355
		decid. forest vs. conif. forest	1.24	0.81	0.74 - 2.04	0.559
		decid forest vs. shrub	1.26	0.79	0.87 - 1.81	0.328
		decid. forest vs. grass	**1.49**	**0.67**	**1.01 - 2.20**	**0.080**
		decid. forest vs. agric	**11.08**	**0.09**	**2.32 - 52.89**	**0.007**
		decid. forest vs. disturbed	**1.67**	**0.60**	**1.06 - 2.62**	**0.050**
		decid. woodl. vs. conif. forest	1.33	0.75	0.85 - 2.08	0.316
		decid. woodl. vs. decid. forest	1.09	0.92	0.76 - 1.56	0.739
		decid. woodl. vs. shrub	**1.37**	**0.73**	**1.22 - 1.54**	**<0.001**
		decid. woodl. vs. grass	**1.63**	**0.61**	**1.38 - 1.93**	**<0.001**

Table 43 (continued). Parameter estimates converted to odds scale for Model 2: cougar nocturnal resource selection at the discrete choice scale in the Oquirrh Mountains, Utah.

Model	Variable	Contrast test for categorical variables	Odds ratio (OR)	1 / OR	95% confidence interval on OR	FDR corrected p-value
0.128(edge) - 0.002(d_strm) +		decid. woodl. vs. riparian	1.09	0.92	0.4 - 2.91	0.910
1.308(LC_rock) + 0.042(LC_conifF) +		**decid. woodl. vs. agric**	**12.10**	**0.08**	**2.64 - 55.54**	**0.004**
0.247(LC_decidF) + 0.335(LC_decidW)		**decid. woodl. vs. disturbed**	**1.83**	**0.55**	**1.37 - 2.44**	**<0.001**
+ 0.376(LC_conifW) + 0.018(LC_shrub) -		conif. woodl. vs. conif. forest	1.39	0.72	0.84 - 2.33	0.316
0.154(LC_grass) + 0.253(LC_ripar) -		conif. woodl. vs. decid. forest	1.14	0.88	0.74 - 1.75	0.680
2.16(LC_ag) - 0.006(slope)		conif. woodl. vs. decid. woodl.	1.04	0.96	0.81 - 1.33	0.817
		conif. woodl. vs. shrub	**1.43**	**0.70**	**1.12 - 1.84**	**0.013**
		conif. woodl. vs. grass	**1.70**	**0.59**	**1.27 - 2.27**	**0.001**
		conif. woodl. vs. riparian	1.13	0.88	0.42 - 3.07	0.865
		conif. wood. vs. agric	**12.61**	**0.08**	**2.70 - 58.85**	**0.004**
		conif. woodl. vs. disturbed	**1.90**	**0.53**	**1.32 - 2.75**	**0.002**
		shrub vs. grass	1.19	0.84	0.99 - 1.43	0.110
		shrub vs. agric	**8.81**	**0.11**	**1.92 - 40.35**	**0.013**
		shrub vs. disturbed	1.33	0.75	0.99 - 1.78	0.095
		grass vs. agric	**7.42**	**0.13**	**1.61 - 34.20**	**0.022**
		grass vs. disturbed	1.12	0.89	0.82 - 1.53	0.604
		riparian vs. conif. forest	1.23	0.81	0.42 - 3.70	0.792
		riparian vs. decid. forest	1.01	0.99	0.35 - 2.86	0.992
		riparian vs. shrub	1.27	0.79	0.47 - 3.45	0.739
		riparian vs. grass	1.49	0.67	0.56 - 4.00	0.559
		riparian vs. agric	**11.14**	**0.09**	**1.82 - 68.17**	**0.021**
		riparian vs. disturbed	1.68	0.60	0.61 - 4.66	0.448
		disturbed vs. agric.	**6.67**	**0.15**	**1.43 - 33.33**	**0.031**
	slope		**0.94**	**1.06**	**0.91 - 0.98**	

woodland, deciduous forest, and riparian (Table 43). Odds of using rocky areas were from 3.5 to 3.6 times greater than odds of using coniferous forest and shrubland types, and from 4.3 to 4.8 times greater than odds of using grassland and disturbed types. Odds of using rocky area were 32 times greater than odds of using agricultural areas; however, the upper confidence limit was large, which may be a reflection of the low likelihood that these 2 types occur adjacent to each other on the study site (and thus in the same choice set).

Generally, odds of using open types (grassland, agriculture, shrubland, and disturbed) were less compared to the odds of using forest and woodland types. Agriculture was highly avoided compared to all other cover types, where the odds of using other cover types (excluding rock, which is discussed above) ranged from 7 to 12 times greater than odds of using agriculture (Table 43). However, cougars with home ranges that bordered agricultural lands were documented in these areas during nocturnal hours.

Model Validation. – The top-ranking and most parsimonious models for each scale and behavior were cross validated to assess model predictive performance. Based on Spearman-rank correlations, all models appeared to predict cougar use well because area-adjusted frequencies from cross-validated use data were positively correlated with binned predictive values (Table 44). The positive correlation indicated that more cougar use locations were falling within the higher predicted values, which represent higher probabilities of use. The home range scale models tended to be slightly more reliable in terms of predictive performance compared to the discrete choice scale models for daybeds and nocturnal use. This was reflected in the higher correlations relative to the

same behavior at the discrete choice scale (Table 44). However, for cache site models, the discrete choice scale models were slightly more reliable than home range scale modes.

Table 44. Cross-validated Spearman-rank correlations between Resource Selection Function bins and area-adjusted frequencies for 5 individual cross-validation sets and their average. Cougar resource selection models were examined for 3 behaviors (prey caching, resting at a daybed, nocturnal activities) and 2 scales of availability (home range scale and discrete choice scale).

Home range scale				Discrete choice scale			
Cross-validation set	Spearman's Rho	95% LCL [a]	95% UCL [b]	Cross-validation set	Spearman's Rho	95% LCL [a]	95% UCL [b]
Cache				Cache			
1	0.956	0.819	0.989	1	0.974	0.890	0.994
2	0.938	0.755	0.986	2	0.963	0.847	0.991
3	0.967	0.861	0.992	3	0.966	0.857	0.992
4	0.951	0.803	0.989	4	0.974	0.889	0.994
5	0.965	0.855	0.992	5	0.974	0.889	0.994
Average	0.955	0.819	0.990	Average	0.970	0.874	0.993
Daybed				Daybed			
1	0.988	0.946	0.997	1	0.925	0.707	0.982
2	0.989	0.952	0.997	2	0.925	0.709	0.983
3	0.989	0.953	0.998	3	0.920	0.690	0.981
4	0.989	0.951	0.997	4	0.917	0.679	0.980
5	0.986	0.941	0.997	5	0.915	0.672	0.980
Average	0.989	0.949	0.997	Average	0.920	0.691	0.981
Nocturnal				Nocturnal			
1	0.976	0.897	0.994	1	0.954	0.814	0.989
2	0.977	0.902	0.995	2	0.942	0.768	0.987
3	0.974	0.890	0.994	3	0.914	0.670	0.980
4	0.967	0.862	0.992	4	0.921	0.694	0.982
5	0.970	0.894	0.994	5	0.952	0.804	0.989
Average	0.973	0.889	0.994	Average	0.937	0.750	0.985

[a] LCL = lower confidence limit
[b] UCL = upper confidence lmit

Predictive ability appeared to be consistent within models since the lines for the 5 cross-validation sets were close together and fairly parallel in each of the plots (Figure 24, Figure 25, and Figure 26). However, cache site models appeared to have slightly more variation in predictive ability across the 5-fold cross-validation sets compared to daybed and nocturnal activity models (Figure 24). Discrete choice scale models for daybed selection may not be as stable at high predicted values as evidenced by the slight drop in frequency values in bins 9 and 10 (Figure 25), and in the lower correlation values (Table 44). Discrete choice scale models for cougar nocturnal activity were least reliable of all models, particularly at low predicted values, because there was a fairly high frequency of cougar use locations in these lower bins (Figure 26). However, there was still a positive correlation overall. The daybed model at the home range scale appears to be the most reliable for predicting cougar use for this behavior. The cross-validated daybed models demonstrated both low frequency in lower bins of predicted values and higher frequency in higher bins, and with consistent patterns across all 5-fold datasets. However, all models for each behavior and scale appeared to predict cougar use well as indicated by the high values of the Spearman-rank correlations, relatively narrow 95% confidence intervals, and high values for the lower confidence limit (lowest value was 0.670).

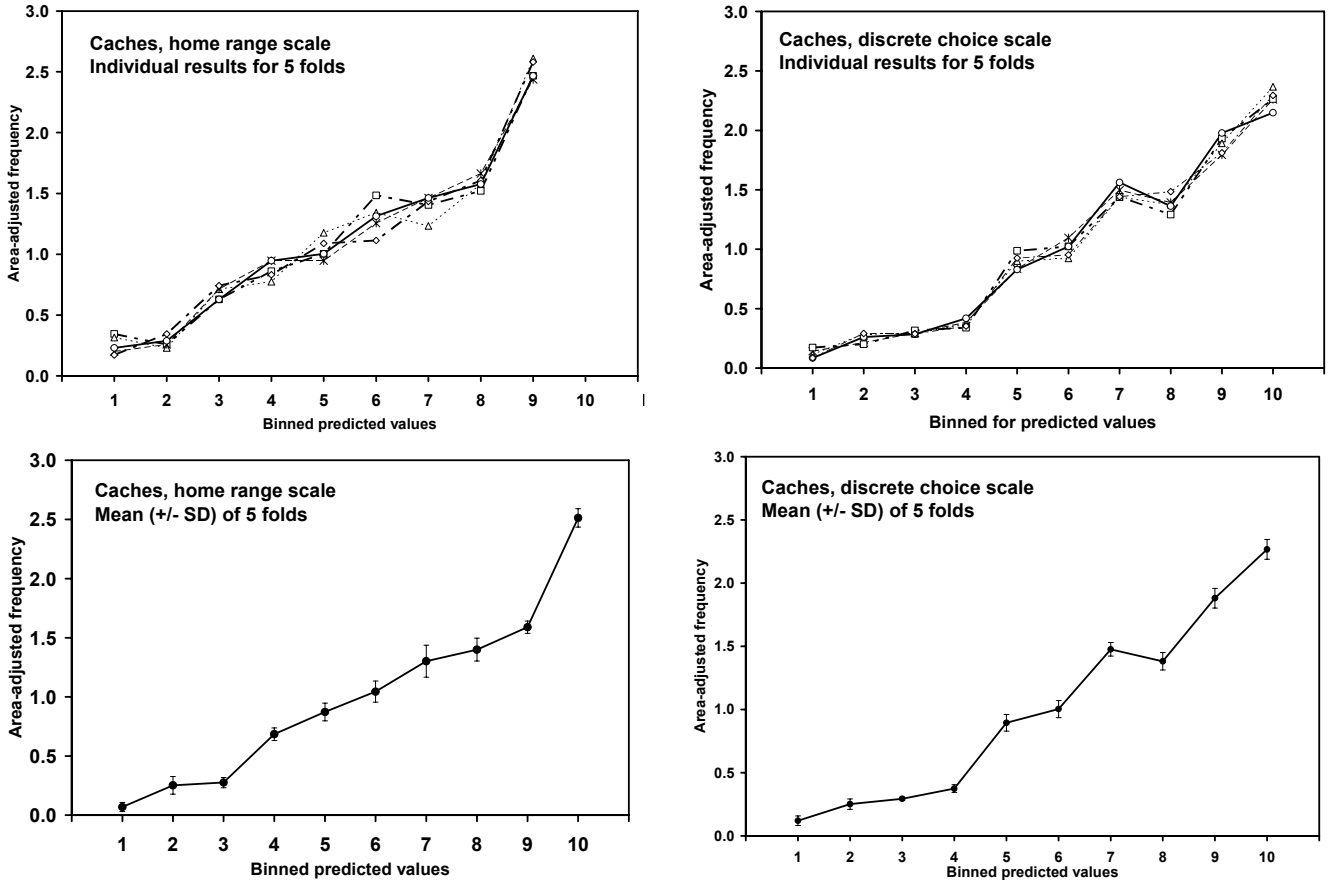

Figure 24. Area-adjusted frequency of binned predicted values from cross-validated use locations in a model of cougar cache site selection. Home range and discrete choice scales of availability were considered. Individual results from a 5-fold cross-validation are presented in the top panels. Mean (+/- SD) frequency values for the 5 sets are presented in the bottom panels.

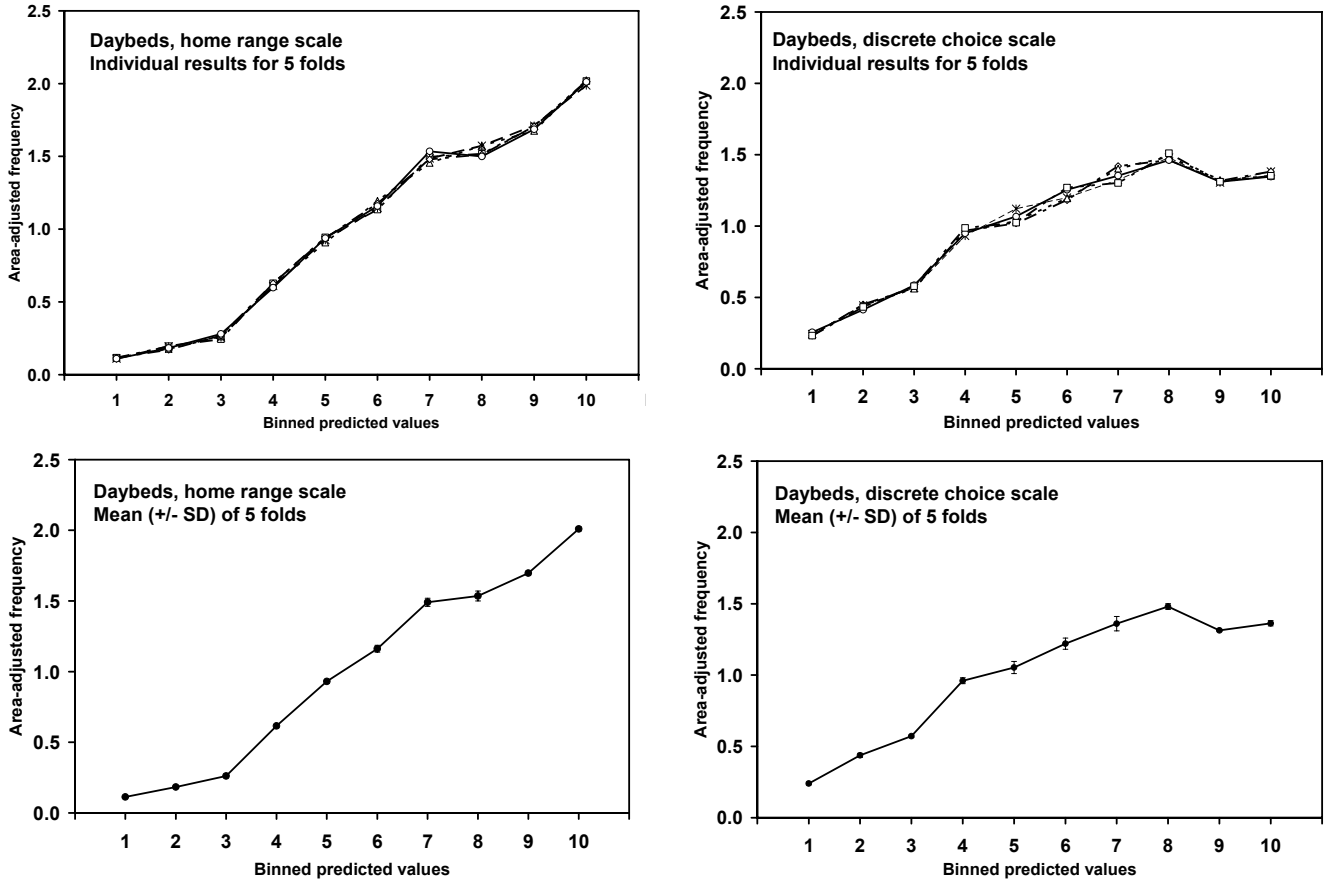

Figure 25. Area-adjusted frequency of binned predicted values from cross-validated use locations in a model of cougar daybed selection. Home range and discrete choice scales of availability were considered. Individual results from 5-fold cross-validation are presented in the top panels. Mean (+/- SD) frequency values for the 5 sets are presented in the bottom panels.

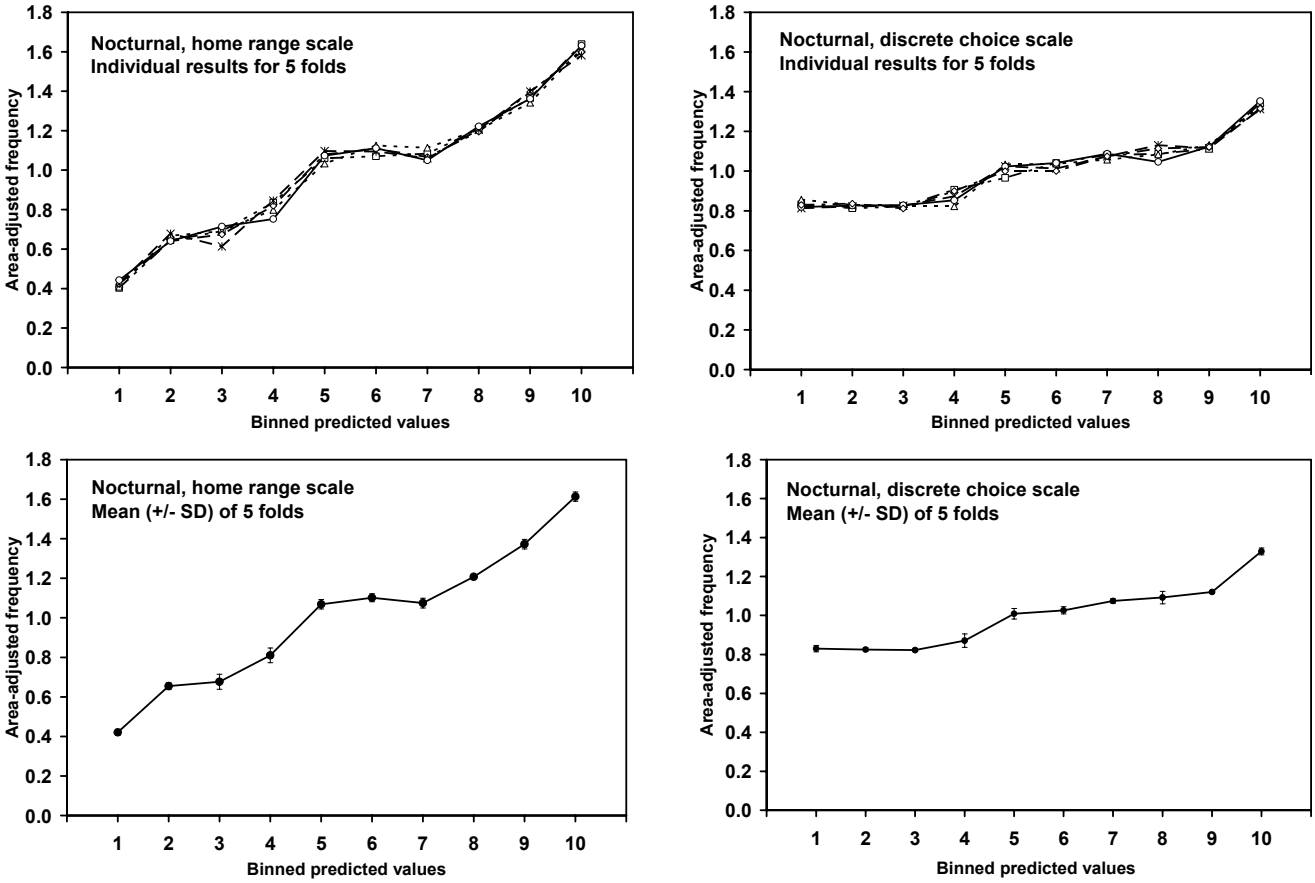

Figure 26. Area-adjusted frequency of binned predicted values from cross-validated use locations in a model of cougar nocturnal resource selection. Home range and discrete choice scales of availability were considered. Individual results from 5-fold cross-validation are presented in the top panels. Mean (+/- SD) frequency values for the 5 sets are presented in the bottom panels.

DISCUSSION

Telemetry

The amount of error associated with an aerial telemetry location varied substantially among test cases, and was likely influenced by weather, terrain, pilot experience, and pilot effort (Hoskinson 1976, Gantz et al. 2006). For example, errors were smallest (within 275 m) for flights conducted by the most experienced pilot when he knew he was being tested, a result also reported by (Gantz et al. 2006). The analysis of cougar resource selection as quantified by aerial telemetry locations was likely more limited by the location error than the resolution of the resource GIS data (e.g., land cover). Although I did not test for variables that might bias the fix rate of the aerial telemetry, fix rate was not uniform since not all cougars were detected on every flight. In addition, there was variation between study sites because a greater proportion of collared cougars were detected during flights over the Oquirrhs site than over the Monroe site (D. Stoner, personal communication).

In general, 95% of locations acquired with GPS receivers should be within 10 m of the true location (Rodgers 2001). Based on the mean and standard deviation of the error estimates, the coordinates acquired by the GPS collars used in this study were approximately 40 times more accurate and 30 times more precise than the aerial telemetry data. The accuracy of any particular GPS location was not always related to the DOP value or the presence of an elevation value, a result also reported by D'Eon and Delparte (2005). However, these variables were indicative of the precision of the overall dataset. For the coarse scale resource selection analyses, a 100-m error buffer around

cougar GPS locations was liberal given that this was 6.5 times the mean error from stationary tests and 99% of errors from these tests were less than 100 m. This size was intended to account for classification errors in the resource GIS data, which would potentially be problematic if attributing a cougar GPS location to a single grid cell. Because the mean GPS error was smaller than the grid cell size of the land cover and other resource GIS data, the analysis of cougar resource use as measured by GPS locations was likely more limited by the resolution of the GIS data than the accuracy of the GPS telemetry.

Fix rates for GPS collars worn by live cougars were similar to those reported for cougars in Wyoming (Anderson and Lindzey 2003). The low fix rate for the 2005-2006 season was likely a result of locations being scheduled more than 4 hours apart. In this situation, the collar had to acquire new satellite ephemeris data, which can take considerable time (up to 12 minutes) and battery power, and decreases the likelihood of acquiring a fix (Rodgers 2001). Cain et al. (2005) reported that fix interval affects fix success rates, particularly as the interval gets further apart.

A consistent temporal bias was present in GPS collar fix rates among all cougars. Lower fix rates during diurnal periods may be attributed to cougar behavior because during these hours cougars were most likely resting in a reclined position. D'Eon and Delparte (2005) found that in controlled tests with stationary collars, the largest source of variation in fix rate and location error with GPS collars was the position of the radio-collar. When the angle of the antenna is greater than 90 degrees from vertical, it may be a large source of data loss (D'Eon and Delparte 2005). For this reason, an animal's activity level and posture can bias the fix rate of a GPS collar (D'Eon 2003). During

nocturnal and crepuscular times cougars were likely hunting and thus moving in a posture that would have placed the collar antennae in the optimal vertical position. In addition to antennae position, the temporal fix rate bias may have been due to differences in signal interference resulting from differential use of vegetation types. During diurnal hours cougars tend to rest in dense cover and during nocturnal hours they will more often enter open areas (Dickson et al. 2005). Anderson and Lindzey (2003) found no differences in fix rate over different times for GPS collars worn by cougars; however, they programmed their collars to attempt fixes predominantly during nocturnal and crepuscular hours.

Surprisingly, the results of the seasonal analysis indicated that fix rates were highest in warmer months when leaf cover would be most likely to interfere with the GPS signal. Because the fix rate was usually lowest in winter and most of the dense overstory vegetation on the Oquirrhs study site is deciduous, it is unlikely that vegetative cover strongly biased the fix rate of the GPS collar data used in this study. The low fix rate in winter may have been due to cougar use of the numerous mineshafts, buildings, and road culverts on the Oquirrhs site to escape cold temperatures, the use of which would likely have blocked the GPS signal. Connolly (1949) documented that cougars in mountains of Utah and Nevada regularly used caves, mineshafts, and abandoned buildings in winter months but not in summer months. Cougars were documented using mineshafts and buildings during this study based on tracks and direct sightings in the field (D. Stoner, personal communication). The pronounced peak in GPS fix rate in spring may have indicated more frequent activity by cougars attempting to track deer as they moved from wintering to fawning range. Migratory mule deer are known to experience greater predation pressure compared to resident deer (Nicholson et al. 1997).

These combined results suggest that the largest source of variation in GPS fix rate was cougar behavior and activity level and their influence on signal interference and antennae position. In both the coarse-level and the fine-level resource selection analyses, the GPS data were analyzed separately by time of day. This should have controlled for the temporal fix rate bias. The resource selection analyses were not conducted separately by season because not all cougars had sufficient data available across all seasons.

Home Range Estimation

Multi-year Diurnal Home Ranges from Aerial Telemetry

Home range estimates from this study did not always reach an area asymptote, indicating that the home ranges generated from fewer than about 40 radiolocations may have been underestimated with the minimum convex polygon (MCP) algorithm. Twenty five percent of home ranges from the Monroe site, and 6% from the Oquirrhs site were estimated with fewer than 40 locations. In addition, the results from linear regression indicated that neither MCP nor fixed kernel (FK) home range size variation was explained by number of radiolocations. Simulation studies have indicated that the FK algorithm is relatively insensitive to differences in sample size (Seaman et al. 1999, Kernohan et al. 2001). Based on these evaluations, the majority of the home range areas estimates should be reliable and therefore appropriately used to define boundaries in the resource selection analysis.

Home range size varied foremost between the sexes. This was not an unexpected finding since other cougar studies have consistently confirmed that male home ranges

may be from 1.5 to 5 times larger than female ranges (Logan and Sweanor 2001). This area is larger than would be predicted based on body size and energetic needs (Sandell 1989). Because cougars are polygynous, breed year-round, have a variable estrus cycle within and among females, and occur in low densities, a male cougar must constantly travel through a large area to monitor the breeding status of females in his range (Logan and Sweanor 2001).

Both male and female cougar home ranges on the Oquirrh Mountains were small relative to those reported for other western North American populations (Logan and Sweanor 2001, Pierce and Bleich 2003). The average MCP home ranges for both sexes on the site were comparable to those estimated for cougars in the Diablo Range in California (84 km^2 Female, 199 km^2 Male; Hopkins 1989), the Klondyke-Aravaipa area of southeastern Arizona (109 km^2 F, 196 km^2 M; Cunningham et al. 1995), and the San Andres Mountains in New Mexico (70 km^2 F, 194 km^2 M; Logan and Sweanor 2001). These study areas were in arid to semi-arid climates with little snowfall, mountains of moderate elevation, and vegetation dominated by woodlands rather than dense forest. Home ranges estimated for female cougars on Monroe Mountain were of moderate size compared to those reported for females in western North America. The average female MCP was comparable to those estimated for cougars in the Rocky Mountains of Alberta (140 km^2; Ross and Jalkotzy 1992), Colorado (126 km^2; Anderson et al. 1992), and Montana (202 km^2; Murphy 1983), as well as the mountains of eastern Nevada (178 km^2; Ashman et al. 1983). These study sites were all located in rugged, forested mountains that received heavy winter snow.

The comparisons above suggest that variation in home range size among cougar populations may be partially explained by seasonal changes in prey density and distribution (Grigione et al. 2002). This may also explain variation within a population (Pierce et al. 1999). Cougars on the Oquirrhs site exhibited 3 types of migratory movements: (1) full migration (moving between separate winter and summer home ranges), (2) partial migration (shifting elevation seasonally within a single home range), and (3) no migration (inhabiting the same area and elevation year-round). These migrations were likely related to the timing of prey movement. In general, cougars with the largest home ranges on the Oquirrhs were fully migratory, those with the smallest ranges did not migrate, and those with ranges closer to the average were partially migratory. This differs from the findings of Pierce et al. (1999), who report that home ranges were larger for cougars that shifted seasonally and smaller for cougars that used disjunct seasonal ranges. On Monroe Mountain, the predominant response to seasonal changes in prey density was elevation shifting, though a few cougars used the same area year-round. It is not clear why no cougars on Monroe Mountain had disjunct seasonal home ranges, but compared to the Oquirrhs ungulate prey may be less concentrated in winter due to greater expanses of winter range in the foothills and valley, which are undeveloped.

Home ranges on the Monroe site were larger on average than those on the Oquirrhs. This suggests that prey were more dispersed in all seasons on Monroe and, given the greater variation in home range size, that prey were more unevenly distributed across the Monroe study site versus the Oquirrhs. In areas with deep snow cover, the amount of winter range available may be a factor limiting cougar populations. However,

this would also depend on ungulate densities since a high degree of overlap in cougar home ranges has been documented when prey are highly concentrated (Traverse Range/Camp Williams in this study; Pierce et al. 1999). The larger average home range size on Monroe compare to the Oquirrhs may also be correlated with the relative amount of ungulate winter and summer range. The Monroe site has a proportionally larger area with deep winter snow cover compared to the Oquirrhs, and thus has a greater area of summer range available once snow melts. In this situation, it is not surprising that cougars used a larger area to meet annual requirements, expanding the area used in the summer as prey became more dispersed. Seidensticker et al. (1973) reported that cougars in the mountains of Idaho used a larger area in summer than in winter. Cougar home range use in the mountains of southern Utah also followed this pattern (Lindzey et al. 1989). Managers should consider separate seasonal cougar density estimates and distributions in areas where prey concentrate during a specific season (Pierce et al. 2000b).

Many cougar studies have reported extensive home range overlap among female cougars and male-female cougars but little overlap among male cougars, a result also documented in this study. However, some studies have reported high overlap among male cougars as well (Anderson et al. 1992, Logan and Sweanor 2001). In this study only three male home ranges were estimated, and these individuals were only monitored for one year; therefore, it is possible that more overlap occurred than was indicated by the available data. Logan and Sweanor (2001) hypothesized that a greater degree of male overlap may be documented if studies had larger sample sizes and were able to capture and track all adult males for a sufficient time to be able to quantify a home range.

The combination of small home range size and high degree of overlap may be an indicator of the best habitat in solitary mammals, and is a situation where a species is likely to be most tolerant of conspecifics (Anderson 1987, McLoughlin et al. 2000). For example, largest home range overlap and smallest home range sizes occurred in brown bear populations located in the best habitat (McLoughlin et al. 2000). However, differences in hunting regimes may confound comparisons of overlap among populations. Although there was more extensive home range overlap among females on the Oquirrhs compared to Monroe, females on the Oquirrhs had longer life spans, less turnover, and were often philopatric (i.e., remaining in the natal area near mother and/or sisters) as a result of the lack of hunting. Although home ranges may overlap spatially, Logan and Sweanor (2001) reported that cougars in the study appeared to avoid interaction by using overlap areas at different times. Females tended to overlap temporally more frequently than males, especially when related (Logan and Sweanor 2001). When males did interact, it was more likely to result in a fatality as they defended their home range and access to females (Logan and Sweanor 2001).

The similarity in home range boundaries between females on the Kennecott property north of the Bingham pit (Oquirrhs site) is likely a function of the geographic constraints of the mountain range. The Oquirrh Mountains are relatively small, and island-like because the range is surrounded by land use and land cover types unsuitable for cougar occupancy. The range itself also contains edges from disturbance due to mining and military activities. Laing (1988) found that topography influenced home range boundaries of cougars in southern Utah. The Monroe site has no areas of widespread disturbance that would disrupt the continuity of habitat, and the mountain is

also larger in size than the Oquirrhs, thus there was greater variability in the placement of home ranges. In addition, the high degree of habitat connectivity around the Monroe study site is evident by cougar home ranges that included adjacent mountain ranges. No home range on the Oquirrhs spanned adjacent ranges. Cougars on the Oquirrh Mountains probably comprise a distinct subpopulation because it is an isolated mountain range linked to other ranges only by immigration and emigration (Stoner et al. 2006). Even though some cougars on the Oquirrhs were migratory, they did not leave the range or interact with cougars from other mountain ranges as occurred in a Sierra Nevada population (Pierce et al. 2000b). However, on Monroe the connectivity of habitat resulted in individuals overlapping management units, and subpopulations in the area probably occur more as gradients than as distinct units even though no cougars made seasonal migrations. Where home ranges spanned adjacent mountain ranges on Monroe may indicate movement corridors used by dispersing cougars. No female cougar had a home range that spanned both sides of a main ridge (though both male cougar ranges on the Oquirrhs crossed ridgelines). Black bears in North Caroline avoided ridges when placing home ranges, which the authors suggested was due to both energetic constraints of traveling over steep terrain and food resources being at highest density at mid-slopes (Powell and Mitchell 1998).

There was no association between home range size and vegetation type except that the largest home ranges occurred on the southern end of the Monroe site where sagebrush-steppe occurs in extensive swaths. Within and among other cougar populations, only very large differences in home range sizes have been correlated with vegetation, where very poor deer habitat (dry, desert shrub or extensive rock) has been

associated with the larger cougar home ranges (Anderson 1983, Laing 1988, Logan and Sweanor 2001). However, Nilsen et al. (2005) compared data from 17 cougar studies and found that neither indices of seasonality or primary productivity were predictive of cougar home range sizes among populations. If any univariate relationship is present between vegetation and home range size, it appears to be a coarse association or only important if habitat is extremely poor. In this study, no cougar had a home range located exclusively in high-elevation forests; rather home ranges were centered on or occurred exclusively in the mid-elevation vegetation band. Lindzey et al. (1989) also found that all cougar home range in southern Utah mountains included ungulate winter range. This suggests that cougars required some minimum amount of winter habitat in or near where prey congregate in winter.

One major difference between the 2 sites in this study was the hunting regime in that Monroe Mountain was open to cougar hunting whereas the majority of the Oquirrhs was protected. This may have resulted in the larger home range sizes on Monroe as a response to density reductions. However, studies that have experimentally removed cougars found that females did not expand home ranges in response to the removals (Laing and Lindzey 1991, Logan and Sweanor 2001). It seems unlikely that hunting influenced female home range size. If a female is already meeting food and cover needs with a small home range there would be no reason for her to use a larger area (Logan and Sweanor 2001). In contrast, male cougars may expand their home range following the removal of males or females in order to maximize breeding success via access to greater number of females (Seidensticker et al. 1973, Maehr et al. 1991, Logan and Sweanor 2001). Logan and Sweanor (2001) compared 5 cougar populations and found no

relationship between cougar density and home range size except at very low densities. However, there is some indication female density may be inversely related to home range size (Weaver et al. 1996). Cougars are probably more influenced by changes in prey density than the presence of other cougars (Pierce et al. 2000b, Logan and Sweanor 2001).

Cougar home range size varies dramatically across the range of the species, which is likely an adaptation that allows the cougar to maintain a broad geographic distribution over diverse environmental conditions (Pierce et al. 2000b). Home range size is likely a function of multiple interacting variables, including intraspecific and interspecific competition, primary productivity as it relates to prey density, vegetation structure as it relates to security cover, landscape heterogeneity as it relates to prey vulnerability, and climate as it relates to the distribution and movement of prey (Seidensticker et al. 1973, Laing 1988, Logan and Sweanor 2001, Pierce and Bleich 2003). Because of seasonal effects, larger home ranges sizes in cougars may not always equate with poor habitat. Density may be a better method of quantifying the area required by a population rather than home range size because variation in density can be explained by energetics whereas variation in home range size cannot (Jetz et al. 2004).

Annual Home Ranges from GPS Collar Data

The average size of annual GPS home ranges was similar to the average size of the multi-year aerial telemetry home ranges on the Oquirrh Mountains. Logan and Sweanor (2001) also report that a cougar's lifetime home range was similar to the largest estimated annual home range size. However, it is probable that had GPS been used to

monitor cougars for the same length of time as the aerial telemetry then the GPS home ranges would have been larger. This is because a greater number of locations and shorter sampling intervals are possible with GPS collars. Some annual GPS home ranges were twice as large as multiyear aerial telemetry home ranges. Typically, only after an individual was monitored for at least 5 years did the area estimated with aerial telemetry approach that covered by GPS in a single year. Based on GPS collar data, Bleich et al. (2000) also suggested that previously published home range estimates derived from aerial telemetry have underestimated the actual area that cougars used.

Larger nocturnal home ranges were a result of more expansive movement during nocturnal periods. There was possibly a sample size bias for MCP estimates since there were a greater number of nocturnal locations than diurnal. However, cougars are typically inactive during diurnal hours (Beier et al. 1995); therefore acquiring more locations would have been ineffective if cougars remained at the same daybed site. Differences in sample sizes should not have affected FK estimates (Seaman et al. 1999). Nocturnal data generally expanded home range boundaries in all directions. Cougars with the largest differences in nocturnal and diurnal home ranges increased use of lower elevations from 1-2 km beyond that used during diurnal hours. These areas often consisted of sagebrush, grass, disturbed, buildings, and industrial areas associated with the processing of mining materials. Similar results were documented in the Sierra Nevada, where cougars rested in steep topography at higher elevations during the day but hunted at night in gentler terrain at lower elevations (Pierce et al. 1998). An expansion of the area used by cougars during nocturnal hours may depend on the types and uniformity of vegetation and topography, as well as prey density and distribution. Studies in other

regions should determine if cougar nocturnal and diurnal space use differs, particularly if use of resources may also be different during these times, or if cougars inhabit home ranges adjacent to human habitation.

Similar to the sex differences in multi-year and annual home ranges, the area (MCP) used by male cougars over a month was 3.5 times the area used by females over this time span. In addition, male cougars appeared to use a greater proportion of their total home range each month than did females and thus covered a larger area in a shorter time period. This suggests that home range area for males may asymptote over a shorter time period than females. Over a 1 month period males covered approximately half of the total home range, and boundaries were similar from month to month. These patterns were likely a result of attempts to maximize access to females in his range. Female monthly MCP home ranges indicated that the boundaries used each month varied, and in any one month a female did not use her entire annual home range. Boundaries of consecutive months were more similar than boundaries from months in different seasons, indicating a gradual shifting of female activity centers into different areas of her range.

Monthly MCP boundaries indicated that both male and female cougars used their home range unevenly, shifting the focus of their activity into different areas of their home range in different months. The complexity in the internal structure of home ranges probably indicated variation in resources within a cougar's range, such as deer abundance, cover for resting during daylight hours, and optimal stalking conditions. Because cougars are solitary hunters, it is also possible that multiple foci in female cougars were the result of attempts to avoid other cougars with overlapping home ranges so as not to interfere with each other's hunt (Kruuk 1986). Using multiple foci may also

serve to maintain the element of surprise when hunting prey within the home range. Multiple activity foci in males appeared to be a result of the distribution of females within his home range. Within the span of a month, males visited all areas of their home range whereas females were more likely to focus activity only in one area during that time period. Female activity centers over an annual period were highly influenced by whether she bore kittens. Surprisingly, only about half of cache sites in this study were located in areas with the densest locations, thus areas with concentrated activity must offer some other advantage beyond food resources, such as shelter. Although core area estimates have been used in conservation planning for some species (Bingham and Noon 1997), for cougar it is probably more appropriate to consider total annual area since they need the large areas to provide an adequate prey base and hunting conditions.

The criteria used to identify natal den sites in this study appeared reliable based on field evidence verifying the presence and age of kittens. It was important to detect both the drop in monthly home range size and the clustering of locations to identify a natal den. While home range size among females was variable prior to the initiation of denning, they were all consistently small post-birth. Previous studies have reported a decrease in cougar home range size when females have young kittens because mothers must stay nearby while nursing (Seidensticker et al. 1973, Maehr et al. 1989, Ross and Jalkotzy 1992, Logan and Sweanor 2001). A female's home range increases 2-3 months after the birth when kittens are weaned and able to travel, and when they also begin requiring greater amounts of food (Hemker et al. 1984, Hansen 1992, Logan and Sweanor 2001). A female's annual home range was smallest in years when kittens were born, a pattern also noted in female cougars in New Mexico (Logan and Sweanor 2001).

Movement and space use patterns of females with young kittens appeared similar to that described in other cougar populations and other felids (Shaw 1980, Maehr et al. 1989, Knick 1990, Fernandez et al. 2002). Mother cougars may have moved kittens to auxiliary den sites to reduce the possibility of infanticide, a common cause of kitten deaths (Lindzey 1987, Logan and Sweanor 2001). In New Mexico, most kitten mortality occurred within the first 3 months of birth, and kittens were typically moved from the natal den when kittens were approximately 50 days old (Logan and Sweanor 2001). Scent and other signs of the den possibly become more apparent the longer it is used (Fernandez et al. 2002). In addition, Benson et al. (2008) report that out of a sample of 51 Florida panther den sites none were ever used more than once. This also supports the infanticide hypothesis because such behavior means that den sites that could not be predictably located by conspecifics. Iberian lynx moved kittens spontaneously but also moved them after researchers intruded to tag the kittens (Fernandez et al. 2002), suggesting that this behavior was at least partially for the protection of the kittens. Because auxiliary dens were not far from the natal den site, their use was probably not a result of the mother seeking new hunting opportunities in other portions of her home range. It was puzzling how nursing cougars acquired adequate food when using such a small natal area since during other times they used a much larger range. Maehr et al. (1989) only located 4 deer caches from 2 Florida panthers with small kittens. It is possible mothers relied on smaller prey and fat reserves during this time.

The timing of natal denning in this study followed the typical cougar birth pulse in western North America, which occurs between June and November (Anderson 1983, Laundre and Hernandez 2007). This birth pulse may be related to prey abundance

(Anderson 1983, Maehr 1997, Logan and Sweanor 2001) because mule deer fawning peaks in June and fawns begin moving out of cover in July (Mooring 1989). Pierce et al. (2000a) reported that females with kittens selected fawns over other deer age classes in late summer. Information on cougar natal denning behavior is relevant to management because a birth peak in mid to late summer means that kittens would be 6 months old or younger at the onset of hunting season in Utah. Hunters may mistakenly kill females with young because kittens only accompany the mother approximately 20% of the time when she is traveling (Barnhurst and Lindzey 1989). Orphaned kittens less than 9 months old usually do not survive (Logan and Sweanor 2001).

Resource Selection

Coarse Level: Diurnal Use Versus Availability

Land Cover: Statistical Issues.— Cougars on Monroe Mountain selectively used land cover types at the second order. However, no selection was detected at the second order for cougars on the Oquirrh Mountains. Statistical procedures to control for false positives may have limited the ability to detect selection for land cover types on the Oquirrh Mountains. It is probable that selection was in fact occurring on the Oquirrhs because tests were statistically significant for some cover types (e.g., agriculture, deciduous woodlands) prior to the adjustments for multiple comparisons, and because the selection patterns for these types were highly consistent among all cougars. If the Oquirrhs site had a larger sample size (there were 13 female cougars compared to 20 on Monroe), it is possible that selection would have been statistically significant even after the adjustments to the p-values. Pooling data for males and females would have

increased the sample size but this was not a viable option because different home range sizes were used for the sexes in the random home range simulation. Even if sample size had not been problematic, it is still possible that no selection would have been detected if the entire Oquirrhs site provides adequate resources for a cougar home range.

Sampling problems were also apparent in the third-order analysis because selection was detected only for cougars that had GPS locations. This was true not only for land cover but for all resources analyzed in this study. This suggested that the error associated with the aerial telemetry data contributed to the failure to find selection at this scale for the cougars on Monroe, as well as for cougars on the Oquirrhs that were not tracked with GPS collars. Apparently, buffering radiolocations did not compensate for location error. Increasing the buffer size would have decreased statistical power even further because as the buffers around locations are enlarged, their area encompasses increasingly larger proportions of the home range until ultimately use equals availability. Differences in sample sizes also could have influenced the ability to detect selection with GPS versus aerial telemetry data. Larger sample sizes increase statistical power (Nams 1989, Belant and Follmann 2002), and there were typically 3 times as many locations for cougars with GPS collar data compared to those with only aerial telemetry data. Because no selection was detected I assumed that aerial telemetry introduced large, random error but did not bias the data. Studies could be conducted to investigate various factors that might affect the ability to detect resource selection with aerial telemetry.

Land Cover: Second-order Selection.— Despite sampling problems, some significant results emerged. In particular, examining 2 study sites was valuable for comparing selection under different availabilities of land cover types. Cougars on both

Monroe Mountain and the Oquirrhs avoided agriculture when selecting a home range even though deer feed in these areas. There was evidence that cougars on the Oquirrhs tended to avoid agricultural areas when selecting a home range, though the results were not statistically significant. These were large areas that lacked cover, and were often located some distance from the mountain foothills that provided vegetative and topographic cover. The avoidance of agriculture is consistent with previous cougar habitat studies (Dickson and Beier 2002, Laing and Lindzey 1991). However, these results were based on analysis of diurnal telemetry data, and it is possible cougars use agriculture more frequently during nocturnal hours.

Second-order selection differed between the 2 study sites because cougars on Monroe avoided including basin shrublands in their home range, but cougars on the Oquirrhs used this type in proportion to its availability. This is likely because basin shrublands on the Oquirrhs occurred in patches among woodland types while on Monroe the basin shrublands occurred in a homogenous swath at elevations below the coniferous woodland belt. This result emphasizes the importance of considering landscape context and variability within blocks of habitat rather than selection for a single vegetation type.

I used circular shaped simulated home ranges for their simplicity and ease of calculation. One possible improvement would be to use the actual shape of each cougar's home range to sample the landscape within the study areas. However, this would have significantly increased computation time. Furthermore, some cougar home ranges were oddly shaped (e.g., with a long linear section extended in one direction), likely as a response to topographical constraints on the study site. Using such odd shapes would

have made it more difficult to fit a sufficient number of random, simulated home ranges within the boundaries of the study area.

Another difference between the study sites was that cougars on Monroe avoided the developed cover type at the second order while on the Oquirrhs it was neither selected nor avoided. Developed types were uncommon on the Monroe site but occurred primarily in the valley basin. Some cougar home ranges included developed areas on the Kennecott and Camp Williams properties. However, the disturbed cover type was neither selected nor avoided on either site. This cover type was rare on Monroe, thus selection was difficult to assess. On the Oquirrhs, the finding of no selection for or against the developed type could be partially a result of using the fixed kernel home range algorithm because the outer boundaries of some polygons ballooned out from radio-locations to include edges of the Bingham copper pit. Cougars clearly avoid large mining pits since no home range encompassed the Bingham pit. However, home ranges of cougars that inhabited the southern portion of Kennecott included smaller pits in their home range, indicating some tolerance of mining activities if the extent of the disturbance is not large relative to cougar home range size. Avoidance of other disturbed areas was evident in that home ranges on the Camp Williams portion of the Oquirrhs typically excluded the military impact area, which lacked vegetative and topographic cover.

While use of some land cover types differed between the 2 study sites there were some consistencies, namely that home ranges on both sites were primarily composed of lower montane woodlands. That is, home ranges were located either wholly in or positioned such that at least the lower half of the range occurred in the woodland belt, which was primarily coniferous on Monroe (pinyon pine-juniper) and deciduous on the

Oquirrhs (Gambel oak, maple). Winter range is limited to these lower elevations because of snow depths and prey migration; therefore no annual home range would occur solely in high-elevation spruce-fir or aspen forests. This pattern was also apparent in the mountains of southern Utah, where all cougar home ranges included deer winter range (Lindzey et al. 1989). The lower montane woodlands likely provided the highest density of resources (prey numbers and hunting conditions) (Powell and Mitchell 1998). The availability of this type may be a factor that limits cougar home range selection. In addition, cougars may be most susceptible to harvest in woodland areas, particularly where there are high road densities, because most hunting takes place in winter when cougars are restricted to these areas.

Land Cover: Third-order Selection.— No selection was detected at the third order for cougars on Monroe Mountain. On the Oquirrhs site, cougars selected for deciduous woodlands at the third order. Consistent with previous studies (Logan and Irwin 1985, Laing and Lindzey 1991, Dickson and Beier 2002), cougars used shrublands less than expected given availability in their home ranges. These conclusions pertain to cougar selection during diurnal hours when they are typically resting at a day bed site. Cougars may use different land cover types during active behaviors, which typically occur during nocturnal hours.

Deciduous woodlands on the Oquirrhs tended to be multi-layered, providing both overstory and understory cover in which cougars could rest and feed on kills. Deciduous woodland communities also provides important habitat for prey. Mule deer appear to select mosaics of shrubs and trees, and fires that prevent succession of woodlands benefit deer by increasing quantity and vigor of forbs, grasses, and shrubs (UDWR 2003). In

addition, acorns provide important fall mast, and shrubs that are favored deer browse (e.g., *Amelanchier* spp., *Purshia* spp., *Cercocarpus* spp.) occur in association with deciduous woodlands (Beale and Darby 1991, Mackie et al. 2003, MDWG 2004). However, without information on prey densities and distribution, it is difficult to determine if cougars selected areas where deer were most abundant or where deer were easiest to kill. Deciduous woodlands are relatively rare in Utah, comprising approximately 3.5% of the state and 7,735 km^2 (USGS 2004), but where they occur over a large enough extent could support cougars in similar densities as on the Oquirrh Mountains assuming deer densities are comparable. Deciduous woodlands in Utah are believed to be stressed due to alteration of the fire cycle, invasive plants, improper grazing, and energy development (Gorrell et al. 2005).

Results from the Oquirrhs indicated that given availability of both coniferous and deciduous woodlands within home ranges, cougars were 1.5 to 5 times more likely to use the deciduous woodlands. Cougar home ranges on Monroe Mountain were comprised of a high proportion of coniferous woodlands, but deciduous woodlands are limited in this study area. Cougar use of coniferous woodlands is likely a function of the availability of other land cover types, as well as its understory structure and tree density. Laing and Lindzey (1991) found that kills were located most frequently in coniferous woodlands compared to forests or shrublands. However, cougar use of coniferous woodlands depended on structure. Specifically pinyon-juniper types with a rock component and ponderosa pine with oak brush component were used more frequently and open PJ-sagebrush communities were used less frequently than expected (Laing and Lindzey 1991).

Pinyon-juniper woodlands also provide habitat for deer. Unlike the oak scrub, this cover type is common and expanding throughout Utah but its characteristics vary tremendously across its range in terms of tree density and understory structure. Pinyon-juniper provides thermal cover for deer in winter (Wasley 2004), however increases in tree density and reduction in understory cover and diversity degrades its utility to deer (Tausch and Tueller 1977, Miller and Tausch 2001, Wasley 2004). Therefore, not all pinyon-juniper woodlands are comparable, and in general, encroachment of this type into sagebrush shrbulands has resulted in decreased forage for deer (Tausch et al. 1981).

Previous cougar studies have demonstrated cougar selection for other land cover types, such as forests (Laing and Lindzey 1991, Williams et al. 1995) and riparian zones (Dickson and Beier 2002). Cougars on both study sites used forests in proportion to availability at the second order. However, I could not make conclusions about cougar use of forests at the third order because these types were fairly rare on the Oquirrhs, and telemetry error impeded detection on Monroe where forests were more extensive. No selection for riparian land cover types was detected in this study, although this could be due to omission errors in the land cover map as a result of the linear nature of this cover type compared to the resolution of the map. Selective use of riparian zones may be more common in arid climates such as California since other studies have reported use of this type in proportion to availability (Logan and Irwin 1985, Laing 1988).

Support for the use of ecotones was evident in that cougars on both sites selected home ranges with a higher density of edge than expected based on availability. Seidensticker et al. (1973) first characterized cougar habitat as mosaics of forests and shrublands. A mixture of cover and open areas is probably an important characteristic of

cougar habitat regardless of the form of the cover (i.e., woodland versus forest). Where cover is patchy cougars may be more selective in their use of land cover types.

Slope.— Second-order selection of moderate and steep slopes on both study sites essentially indicated home range placement along mountain sides, and avoidance of valleys, plateaus, and high elevation peaks. These mid-slopes are also associated with vegetation that would provide both understory and overstory cover. At the third order, cougars on the Oquirrhs selectively used steep areas and avoided gentle slopes within their home ranges. This is in accordance with cougar use of slope classes in western Wyoming (Logan and Irwin 1985) and southern Utah (Laing and Lindzey 1991), with the exception that extremely rugged slopes were not selected. However, these slopes rarely occurred in the study area. Steep slopes are believed to provide an advantage when killing prey (Logan and Irwin 1985, Jalkotzky et al. 1999) and mule deer also frequent steep slopes (Julander and Jeffery 1964).

Landform.— At the second order, cougars selected home ranges in areas of the study sites with steep and topographically diverse landforms on both study sites. At the third order, and consistent with results reported by Dickson and Beier (2006), cougars in this study selectively used canyons and drainages. Canyons and drainages may offer a thermal advantage in the hot summers by providing cooler temperatures. In more arid areas with patchy cover cougars may also select drainages because the vegetation tends to be denser there compared to other landforms due to moister conditions. Dickson and Beier (2006) suggested that cougars selected for the canyon landform itself and not simply for vegetation classified as riparian because the 2 were not always correlated. This probably applies to this study as well since riparian vegetation was relatively rare on

both study sites. In contrast to descriptions by Seidensticker et al. (1973) that cougars "zig-zag" across drainages, cougars in southern California moved along canyons rather than across them, which may have been a means of reducing energy expenditure (Dickson and Beier 2006).

Fine Level: Modeling Selection During Different Behaviors

Cache Site Models.— Beier et al. (1995) hypothesized that cougars most likely attempt to hide prey remains to reduce both losses to scavengers and the rate of decomposition. Results from the top-ranked resource selection models were consistent with these hypotheses since variables related to concealment cover were most strongly predictive of cougar cache sites at both scales of availability. Variables that influence ambient temperature also appeared to have an effect on cache site selection, which supports the decomposition hypothesis. Fine scale (discrete choice) and coarse scale (home range) cache site models were similar, but edge was explanatory only at the discrete choice scale and elevation was explanatory only at the home range scale.

At the home range scale, cache site selection was likely a function of both areas frequented by prey and areas in the home range where cougars were more successful at killing prey. This is evident in the fact that resources characterizing cache sites differed from resources used during nocturnal hours when cougars would presumably be hunting and moving about more broadly across their entire home range. Because of the relatively fine spatial and temporal scale compared to the home range scale model, the discrete choice model for cache sites is likely a more precise representation of the decisions cougar make about dragging the prey carcass after a kill is made given the choices in a

localized area. Cougars generally drag the prey remains a relatively short distance, if at all (Beier et al. 1995 reported an average of 28 m). Given this fact, the 200-m radius used for sampling available resources for discrete choice models was a relevant scale.

Cougar cache sites were lower in elevations compared to all elevations available in the home range. Mule deer may have been using lower elevations compared to total range of the cougars, and cougars may have been more successful at killing deer at lower elevations. This result was for data pooled over all seasons; however, the pattern could be stronger in certain seasons, particular in winter when deer would be using lower elevations due to snow depths. Pierce et al. (2000b) found that deer kills were clumped within cougar distributions in winter months, which was a result of cougars using higher elevations during the diurnal hours compared to areas used nocturnally. Mule deer and cougar may have greatest overlap at mid-elevations relative to the total distribution of both species, but without information on deer distribution in the study area, this hypothesis cannot be confirmed. Elevation did not explain cache site selection at the discrete choice scale, but this was expected since only small changes in elevation would occur in a localized area. It is difficult to measure enough variation in the environment on a continuous scale if samples are acquired in close proximity to each other.

Cougar selection of southern aspects for caching was contrary to the expectation that cougars would avoid this aspect, particularly at the discrete choice scale, due to the likelihood that the warmer temperatures would accelerate decomposition of the prey remains. Other studies have demonstrated that cougars respond to temperature to when caching prey. Mattson et al. (2007) found that prey remains were more likely to be moved when the kill occurred on southern aspects, and that cougar were more likely to

bury prey remains at a cache site (as opposed to leaving unburied) when ambient temperatures were higher. Beier et al. (1995) determined that cougars in their study usually moved carcasses into shaded areas. It is possible that cougars make more kills in southern aspects due to higher prey densities, but then within these areas optimize the location of the cache depending on local conditions by dragging the remains to a shaded location or canyon landform that provide cooler temperatures. These results imply that there is a tradeoff between reducing the rate of carcass decomposition and the energy required to move a large mass. Deer selectively use aspects, including southern aspects (in winter) and eastern aspects (in summer) (Johnson et al. 2000, Mackie et al. 2003, D'Eon and Serrouya 2005), which supports the hypothesis that location of cache sites and cougar use of aspect was at least partially a function of prey use and distribution.

Cougar selection of canyon landforms for caching prey has been documented in other studies. Beier et al. (1995) reported that caches were commonly located in canyons and riparian areas, and Hopkins (1989) found 73% of all cougar prey caches in creek bottoms. Canyons provide cooler temperatures relative to other topographic positions, as well as denser vegetation to facilitate concealment of prey remains. Additionally, it is possible cougars simply made more kills in canyons since prey species may frequent these areas (Dickson and Beier 2006). However, because the actual kill site was not known in this study, nor was deer distribution, this hypothesis cannot be confirmed.

Canyons may also provide an energetic advantage to moving the prey carcass. If the actual kill were made in a landform adjacent to canyons (i.e., steep or gentle hillsides), it is likely based on previous studies (Beier et al. 1995) that cougars drag the carcass down slope rather than up slope since this would require less energy. The size of

the prey carcass appears to have the greatest effect on whether a cougar moves the remains from the kill site to another area (Mattson et al. 2007), which implies that energy expenditure is an important influence on cache site selection. The avoidance of ridges when caching prey is likely due to their warmer temperatures, more limited vegetative cover, prominence to aerial scavengers, and the likelihood that cougars both attack prey (Jalkotzy et al. 1999) and move carcasses in a downhill direction.

Cougars selected riparian, deciduous woodland, and deciduous forest land cover types at both scales when caching prey. All of these types tend to have both an overstory and an understory layer. Deciduous cover types are also used more frequently by mule deer, which prefer to forage on mahogany, oak, and bitterbrush (Robinette et al. 1952, Pierce at al. 2004, Sandoval et al. 2005). Logan and Irwin (1985) and Mattson et al. (2007) also reported that cougar selectively cached prey in bitterbrush and mahogany communities. Laing (1988) found that caches were located more than expected in rocky areas mixed with pinyon-juniper, but caches were also commonly located in ponderosa pine/oakbrush. In contrast, rock cover types were rarely used for caching in this study; however, Laing's (1988) study site in southern Utah included a larger proportion of open pinyon-juniper habitat than what is present in the Oquirrh Mountains, and rock may have provided cover where vegetative understory was lacking.

Coniferous woodland (i.e., pinyon-juniper) and deciduous and coniferous forest types provide overstory cover but are more likely to lack an understory layer. In this study cougars neither selected nor avoided these habitats when caching prey. Laing (1988) reported that cougars cached less than expected in spruce-fir forests and aspen mixed with spruce-fir. These results suggest that cougar selected vegetative cover for

caching prey based on their concealment characteristics, and not solely for the cooler temperatures provided by an overstory.

The fact that cougars avoided caching prey in cover types that lacked an overstory (e.g., shrublands, grassland, disturbed areas) is evidence that the presence of both overstory and understory cover are favored for hiding prey remains. Mattson et al. (2007) found that cougars were more likely to move a prey carcass to a cache site when the kill occurred in herbaceous vegetation. The larger effect sizes in the discrete choice scale models indicate that cougars were even more strongly selective of these land cover types when making choices at a specific time and given choices available in a localized area.

At the home range scale, cougar neither avoided nor selected edge when caching prey, but at the discrete choice scale cougars avoided caching on edges. The avoidance of edge at fine scales, in conjunction with selection for overstory cover, indicates the cougars tended to drag prey remains further inside a patch of vegetative cover rather than leaving the carcass at the edge of the patch or in a more open area. This is consistent with the concealment hypothesis. Because the location of the kill site relative to the cache site is not known in this study, the effect of edge on the ability of cougar to kill prey cannot be evaluated.

The caching of prey in areas with a greater diversity of vegetation types may reflect the increased likelihood of killing prey in or near areas with a mosaic of vegetation types. Mule deer are known to prefer a mixture of plant species and community types (Julander and Jeffery 1964, Mackie et al. 2003). Furthermore, landscape heterogeneity has been shown to be predictive of mule deer home range size and densities in California (Kie et al. 2002). The fact that land cover diversity did not

explain cougar selection of daybed sites or nocturnal use sites was further evidence that compared to these other behaviors, cache sites were reflective of areas frequented by prey. It was somewhat surprising that diversity was also included in the discrete choice scale model given the resolution of the GIS data used to derive the index. It is possible that a mixture of vegetation types provides variation in height and stem densities at a fine scale, increasing the complexity of cover from multiple directions. Logan and Irwin (1985) and Laing (1988) both reported that cougars used forests with a diversity of age classes and species more frequently than single-age monocultures.

Cougars in the Oquirrh Mountains often rested at daybed sites located far away from their cached prey rather than guarding it, a result also reported by Beier et al. (1995). This behavior is puzzling in light of the effort taken to hide the carcass, but cougars may be attempting to minimize the potential for intraspecific or interspecific conflict. Cougars are known to scavenge (Mattson et al. 2007) but it is not known if they usurp other cougar's kills or kills by other carnivore species. Cougars can be displaced from their cache by other large carnivores, including coyotes, bears, and wolves (Murphy et al. 1999), although of these only coyotes were present in the Oquirrh Mountains. Little is known about the frequency of scavenging of cougar caches (e.g., by other cougars or avian, mesocarnivore, or arthropod species), or the actual amount of biomass loss that may occur.

Daybed Models.— Results from the modeling of cougar daybed selection were consistent with results from previous sections of this study on second and third-order resource selection during diurnal hours. Results from the daybed models support the hypothesis that cougars select daybed sites that provide security and aid in

thermoregulation. Although concealment cover influenced selection of both daybed sites and cache sites, daybeds differed from caches because they were also located at higher elevations, further from roads, and on steeper slopes. Fine scale (discrete choice) and coarse scale (home range) daybed models differed on a number of variables, although variables that were included in both models were consistent in terms of the direction of the effect. Characteristics of daybed sites that support the security hypothesis include the use of areas further from edges (discrete choice scale only), moderately high elevations (home range scale only), moderately steep slopes (both scales), and areas located further from roads (both scales).

As with the discrete choice cache site model, cougar avoidance of edges in conjunction with selection for vegetation types that provide cover indicates they select daybed sites that are deeper within a patch of cover rather than on the edge or in open vegetation. Laing (1988) and Katnik (2002) also reported that, based on diurnal telemetry locations, cougars avoided edge.

Moderately high elevations in cougar home ranges tend to be further from urban, industrial, and other human-dominated areas, and also have greater topographic cover and diversity. However, cougars seemed to avoid the very highest elevations in their home range. The highest elevations may be further from areas where cougars would hunt at night; thus moderate elevations could be selected to limit energy expended when moving from daybeds to lower elevation hunting sites. High elevations in a home range also likely represent ridges and hilltops, which may lack sufficient topographic or vegetation cover to provide security. There was no selective use of elevation at the

discrete choice scale but it is unlikely cougar would distinguish small changes in elevation in a localized area.

Use of relatively steep areas during the day is also consistent with the security hypothesis since steeper areas probably provide a greater sense of protection compared to gentle slopes. This is particularly true since slope was explanatory of daybeds sites at both scales of availability. The quadratic slope term indicated that moderately steep slopes are optimum for cougar daybed sites. This is in contrast to previous studies that reported cougar selected the steepest slopes available (Logan and Irwin 1985, Laing 1988, Jalkotzy et al. 1999). It was also surprising that terrain ruggedness (i.e., standard deviation of slope) was not explanatory of any behavior in this study as cougar affinity for high degree of terrain ruggedness has been reported in previous studies (Jalkotzy et al. 1999, Mattson et al. 2007). This difference from other studies may be due to differences in the range of terrain ruggedness available within various study areas, or methodological differences where studies considered available resources within the entire study area rather than within a home range.

At both scales, cougars avoided roads when selecting a daybed site. The roads in the Oquirrh Mountains study area were predominantly dirt roads. Results from previous studies suggest that cougar use or avoidance of dirt roads during diurnal hours may be dependent on the level of improvement to the road and the level of traffic. Fescke (2003) reported that cougar avoided improved dirt roads during daylight hours but did not avoid unimproved dirt roads. Jalkotzy et al. (1999) reported that cougar did not avoid low traffic dirt roads, but did avoid roads receiving heavier use by people. I did not expect cougars to avoid roads in this study because they are predominantly closed to the public

and vehicular disturbance is minimal. However, I did not classify roads in the study area by surface type or improvement level, and they do vary in these characteristics. On Kennecott's property, roads near the pit and processing areas receive heavy vehicular use at all times of day. Roads on Camp Williams occasionally receive heavy use during military training events, but in general vehicular use is fairly light. Regardless of road characteristics, avoidance of any road is consistent with the security hypothesis, and indicates cougar located daybeds farther from areas with human disturbance.

The selection of rock, deciduous woodland, and riparian land cover types for daybed sites was likely due to these cover types having characteristics that provide hiding cover and optimize thermoregulation. Rocky outcrops provide crevices for hiding, shade in summer, and shelter from snow, rain, and wind. Deciduous woodlands and riparian types provide overstory and understory cover for hiding, as well as shade in summer. Use of similar land cover types has been reported in other cougar studies using diurnal telemetry locations, particularly in areas of cougar range that are comprised of predominantly woodland cover types. Female cougars in northern Arizona preferred rock and oak chaparral (Arundel et al. 2007). Laing (1988) found that areas with prominence of oakbrush and areas with pockets of boulders, lava rock, and sandstone ledges were used preferentially in southern Utah. In southern California, cougars also preferred riparian types during diurnal hours (Dickson and Beier 2002).

Cougar avoidance of open habitat types (e.g., shrublands, grasslands) and developed areas for daybed sites is not surprising since these types do not provide overstory cover for security or aid in thermoregulation. Many other cougar studies have documented this pattern (Logan and Irwin 1985, Laing and Lindzey 1991, Dickson and

Beier 2002, Katnik 2002, Cox et al. 2006). Some studies have documented cougar selection for mixed conifer (Logan and Irwin 1985, Williams et al. 1995, Katnik 2002), pinyon-juniper, and ponderosa pine forests and woodlands (Campbell 1998, Arundel et al. 2007). In this study, cougar selected coniferous forests and pinyon-juniper woodlands over more open types for daybed sites, but deciduous woodlands, rock, and riparian types were preferred above all coniferous types, regardless of the scale of availability. Because all coniferous forests were pooled into one type in this study, I was not able to determine if age class or species diversity affected cougar use of coniferous forests, but these characteristics have been associated with cougar use in other studies.

Cougars did not selectively use aspect when considering availability within the entire home range, but in a localized area aspect appeared to have an effect on cougar choice of a daybed site. Cougar selection of cooler northern and eastern aspects for daybeds supports the thermoregulation hypothesis. However, odds of cougar using southern aspects were even greater than odds of using eastern and northern aspects. Dickson and Beier (2002) reported that cougars did not use aspect selectively during diurnal hours; however, their study area had a mild climate and received little snow. As in the cache site models, there is potentially a seasonal effect where southern aspects would be selected in winter to provide sunny, warm areas for resting at a daybed site, and cooler aspects would be used in summer. Based on diurnal telemetry, Jalkotzy et al. (1999) reported that female cougars selected south and west-facing slopes throughout the year, but males used aspect selectively only in summer, when they preferentially used north and east-facing slopes. In a study area that received heavy snow, cougar selected southwest aspects within their winter home ranges during diurnal hours (Katnik 2002).

Distance to streams was explanatory of cougar daybed selection at the home range scale. The importance of streams to cougars during diurnal hours is unknown, but may vary depending on climate. Beier et al. (1995) documented cougars moving to a water source at dawn after feeding on cached prey. In southern Utah, areas highly used by cougars during diurnal hours tended to be closer to riparian zones (Laing 1988).

Nocturnal Models.— Models of cougar resource selection during nocturnal hours were a function of variables related to energy efficiency, prey use, and facilitation of stalking prey. Elevation did not explain nocturnal use, which implies that cougar used all elevations in their home range when moving about during nocturnal hours (compared to using lower elevations for caching and higher for daybed selection).

The selection of gentle slopes (discrete choice scale) and canyon landforms (home range scale) during nocturnal hours was consistent with the findings of Dickson and Beier (2006) who suggested cougars maximized energy efficiency during nocturnal movements across their home range by moving along contours rather than across them. Notably, use of gentle slopes during nocturnal hours is in contrast to the pattern that was observed in daybed selection, where cougars selected steeper slopes.

Landform was selected similarly for caching and nocturnal activities. Notably, landform was not included in models for daybed selection at either scale; rather landform was used in proportion to their availability during diurnal hours. Because cougars rarely move far during the day (Beier et al. 1995), landform appears to influence cougar resource use primarily when they are active.

Cougar avoidance of northern aspects during nocturnal activities (at the home range scale) is likely a function of prey distribution during crepuscular and nocturnal

hours. Elk reportedly move to southern and western aspects at dusk (Ager et al. 2003). Cougars used all other aspects in proportion to availability.

During nocturnal hours, cougars selected areas closer to streams both at the home range scale and when considering choices available within a localized area. However, in this study cougar did not use riparian vegetation preferentially during nocturnal activities. Previous studies have documented cougar association with riparian vegetation during nocturnal hours (Dickson et al. 2005) but not specifically with streams. Using GPS data from all times of day, Arundel et al. (2007) found cougars selectively used areas closer to water sources, although these were mostly cattle tanks in their study area. At higher elevations, streams would be associated with canyon landforms and riparian vegetation. The positive association with streams may be particularly important at lower elevations, where gentler topography and more open vegetation types limit stalking cover. That is, at lower elevations cougars may be taking advantage of any form of topographic cover, including small washes that that lack riparian vegetation and were not captured as canyons in the landform model. Mule deer also select areas near water (Stewart et al. 2002).

Of the 3 behaviors examined in this study, cougars were least selective of land cover resources during nocturnal hours when they would be using their home range more broadly. During their active hunting periods, cougars selected only for deciduous woodlands and rock cover types at the home range scale. At the discrete choice scale, cougars selected for these types along with deciduous forest. During nocturnal hours, cougars were more likely to avoid open cover types at the discrete choice scale compared to the home range scale, but not as strongly as in other behaviors. Notably there was

strong evidence at both scales that cougars selectively used rock outcrop over all other cover types (including deciduous woodlands) during nocturnal hours, possibly because these areas potentially provides vantage points for sighting prey. Hopcraft et al. (2005) documented Serengeti lions using vantage points, such as rocky outcrops and erosion embankments. The rocky land cover type also included mountain mahogany communities, which are favored foraging areas for deer (Guethner et al. 1993).

As cougar move across their home range in search of prey, they would be more likely to encounter a greater diversity of cover types, including more open types, simply as a result of covering greater distances during nocturnal hours. Though cougars were less likely to avoid open cover types nocturnally compared to other times of day or behaviors, they still preferred deciduous woodlands overall. However, odds of cougar using deciduous woodlands during nocturnal activities were less then odds of using deciduous woodlands for daybeds or cache sites. Other studies that have examined cougar use of land cover during nocturnal hours have documented cougar use of a greater range of cover types during nocturnal hours but also concluded that areas providing cover were selected overall (Dickson et al. 2005, Land et al. 2008).

Although the results of this study indicated that cougar avoided agricultural and suburban areas overall, it is notable that nocturnal and crepuscular hours were the only period of the day when cougars ever entered agricultural and suburban areas. Cougars were documented near residential areas in Copperton and Rose Canyon, and areas adjacent to office buildings of Camp Williams during nocturnal hours. Cougars were also documented within large expanses of grasslands and shrublands at low elevation areas, wetlands associated with Kennecott settling ponds to northeast, and along the

Jordan River. Use of these areas seemed to vary depending on the individual cougar since not all cougars in the vicinity used these areas.

Cougars selectively used edge during nocturnal activities, whereas they avoided edge for daybed and cache sites. Edge was explanatory of cougar nocturnal use at both scales, indicating that cougars actively seek out edges both at larger spatial and temporal scales (i.e., when moving across their home range) and when moving from patch to patch in a localized area. One study used snow tracking to locate actual kill sites, and found that cougar made more kills in edge habitat (Laundre and Hernandez 2003). Edge may provide optimum conditions for stalking prey because cougar can stalk within patches of cover to get close to prey, but visually locate and pursue prey into open areas. Pierce et al. (2000a) reported that cougar killed more deer in open areas compared to areas with greater cover. The use of edge is consistent with the more general use of land cover during nocturnal hours, since edge habitats could be classified as either a land cover type with overstory cover or as one of the more open types.

Cougars were attracted to roads during nocturnal activities, which is in contrast to diurnal habitat use when they avoided roads. Roads may attract prey foraging, and also provide edge habitat for cougar to stalk prey. Elk and mule deer favor areas near dirt roads during crepuscular and nocturnal hours (Johnson et al. 2000, Ager et al. 2003). Most roads in the Oquirrh Mountains study area are dirt roads. Dickson et al. (2005) reported cougars did not avoid dirt roads during nocturnal movements, and may have used them for traveling. Van Dyke et al. (1986b) found that track surveys, which presumably represent cougar nocturnal movements, indicated cougars crossed unimproved dirt roads more frequently than improved dirt road. As stated in the daybed

modeling section above, I did not classify roads in the study area by surface type or improvement level. These characteristics are likely correlated with road width and amount of adjacent cover. As Fescke (2003) suggested, cougar use of areas near roads could be a function of the amount of adjacent cover. Cougars were also documenting crossing paved roads located at lower elevations during nocturnal hours. Road kills are a major cause of death in some cougar populations. Cougars in this study were documented on the lower side of State Road 68 on numerous occasions. Based on tracks observed in the field, they were known to use culverts and underpasses for crossing (D. Stoner, personal communication), but at least 2 cougars in the study area were killed by collisions with vehicles (Stoner 2004).

General Conclusions.— Thermoregulation, energy efficiency, security, prey distribution, and concealment cover all appear to be important factors in cougar resource selection. The results from this study support the concept of cougar habitat as a complex of vegetation, topography, and prey. However, relative use of these features varied depending on scale and the behavior the cougar was engaged in. In some cases a positive association with a resource was documented during one behavior and a negative association with that resource was documented during another behavior. These results emphasize the importance of examining resource selection over different behaviors and times of day for species that potentially use habitat differently for different activities. Using diurnal data to draw conclusions about cougar resource use during nocturnal hours may be misleading. Discrete choice models are more precise and behaviorally driven, and perhaps are a better representation of the choices cougars make at a localized time and place. Because cougars are wide ranging and have large home ranges, they are likely

to respond to the attributes of the environment at multiple scales. They may respond at relatively fine scales when selecting a daybed or cache site or when stalking prey; at meso-scales when selecting a home range; and at regional scales when dispersing.

While there were no contradicting patterns in use of a resource at the 2 different scales, some variables were only explanatory at 1 of the scales examined. Examination of multiple scales may be particularly important for species that move across large areas in relatively short periods of time because availability of resources could change dramatically across a cougar's home range. Based on cross-validation tests, predictive ability of the models was high across the range of behaviors and scales examined in this study. However, testing a model with external, independent data is the most robust form of model validation.

Although, these results indicate cougars avoided disturbed areas at a localized scale, this is a result of using points to assign habitat association. For example, a location adjacent to a building but within a patch of grassland was classified as grassland rather than disturbed, but clearly the cougar was not avoiding the building. Measuring distance to disturbance may have been a better approach to determining cougar response to disturbed cover types. One of the major qualitative findings of this study is that cougar were tolerant of a high level of disturbance in their home range given that multiple cougar home ranges encompassed industrialized areas associated with mining and ore processing facilities. Only the large Bingham pit was avoided as no home range encompassed this area and no cougar with a bordering home range entered the pit. However, cougars used the edges of the pit where sufficient cover was present. For

example, M33 was documented using edges of the pit where mountain mahogany and coniferous trees provided cover.

Even where large areas are highly developed or disturbed, they can still be used by cougars given that cover and prey are available. During nocturnal hours, cougars took advantage of patches of trees within industrialized areas on Kennecott property, and occasionally cached prey in these patches. Cougar use of areas around the Kennecott processing facilities, which run 24 hours a day, is another indication that cougars can habituate to noise and brightly lit areas. Though Beier (1995) stated that dispersing cougars avoided lighted areas, it is possible dispersing cougars are more reluctant to enter lighted areas due to cautiousness in unfamiliar territory. Cougar and deer in the Oquirrh Mountains have had many generations to habituate to mining disturbance since the mine has been in operation since the early 1900s.

Cougar tolerance of disturbance does not negate the fact that the Bingham Canyon Mine's pit (and associated disturbance, such as spoil piles) resulted in habitat loss equivalent in area to 1 female home range, a potentially significant impact to this small population if immigration is impeded (Beier 1996). At least part of the Oquirrh Mountains is vulnerable to residential development due to private land ownership and proximity to Salt Lake City. While high density housing is unusable to cougars (Beier 1995), the impact of low density housing development on cougar habitat quality (i.e., survival and reproduction) is unknown. However, such development would likely result in increased removals of nuisance cougars (Torres et al. 1996).

Modeling Limitations and Future Work.— Available GIS data for land cover and the derivation of edge from land cover were too coarse to use when modeling cougar

decisions made at a fine spatial scale, thus the need for time-intensive aerial photo interpretation used in this study. Photo interpretation reduced errors associated with assigning a point to a single land cover pixel in a GIS layer, because the likelihood of a single pixel accurately representing what is on the ground is low. Furthermore, the minimum patch size visible on aerial photos was much smaller than the minimum mapped by available land cover data. Therefore, the ability to identify edge at a fine-scale was only possible with the use of aerial photos. However, use of photo interpretation limited my ability to generate predictive maps of cougar probability of use in an area, and such maps could aid in land use planning on the Oquirrh Mountains. Potentially, a deductive model could be generated (Stoms et al. 1992) by cross-walking model results to available GIS data; however, such a model would still be limited by resolution and accuracy of land cover data. Other factors not measured in this study may be important to cougar resource selection at an even finer scale (e.g., stem density, percent cover, downed debris) (Laing 1988).

No study has simultaneously documented deer and cougar movements during nocturnal hours. Cougar habitat selection as a function of prey distribution and movement is a major area that is lacking research. Hypotheses regarding overlap of prey and cougar distributions, cougar kill success, and predation rates could be examined. For example, a kill site model could be generated relative to all areas that deer use and all areas that cougar use to determine how landscape features affect prey vulnerability to cougar predation as well as cougar kill success.

Cougars on the Oquirrh Mountains likely use resources differently depending on season, particularly cougars that had disjunct summer and winter home ranges. However,

there is probably little inter-annual variation in cougar resource selection because cougars show high fidelity to their home ranges (Logan and Sweanor 2001). Severe summer drought or winter snow depths potentially could impact cougar resource use as it changes prey distribution.

Future work could also examine differences in resource selection between male and female cougars. Habitat selection could differ between male and female cougars, particular in populations where there are a variety of prey species (elk, moose, mule deer) that comprise different proportions of male and female total kills. Arundel et al. (2007) found that female cougars were more selective of vegetation types than male cougars. The presence and age of kittens may affect resource selection by female cougars. Laing (1988) found habitat use in southern Utah differed between females with and without kittens; females with kittens used habitat with a greater proportion of rock cavities and understory cover. Arundel et al. (2007) reported that females were less likely to use areas frequented by male cougars in the summer, the season when kittens are most likely to be born. In other large, sexually dimorphic carnivores, females altered feeding strategies to avoid interactions with males that may kill cubs (Rode et al. 2006). Pierce et al. (1998) found that female cougars with kittens avoided other cougars by feeding on cached prey remains during diurnal hours. Other age effects could occur, but it is not known if dispersing, subadult, or non-resident cougars that are still attempting to establish home ranges use lower quality habitat.

MANAGEMENT IMPLICATIONS

Aerial telemetry may be of limited utility for resource selection studies in mountainous terrain. Unless managers are interested in examining home range selection, habitat studies should use GPS collars since they provide data with minimal spatial error while acquiring a large number of locations at frequent intervals.

Pooling data over various cougar behaviors may be misleading when examining resource selection. Furthermore, using diurnal data to make conclusions about selection during other times of day may be misleading because cougar behaviors differ over various times of day. Studies in other regions should determine if nocturnal and diurnal space use differs, particularly if cougar in habitat home ranges adjacent to human habitation.

Given cougar propensity for hiding during daylight hours, and avoidance of human dominated areas and roads, encounters with people would be least likely this time of day. Furthermore, cougar low level of activity during diurnal hours further reduces likelihood of encounters with people. Interactions with people are most likely to occur during crepuscular hours when both cougars and people would be active (Sweanor et al. 2008).

While cougars avoided roads during diurnal hours, they did not avoid roads during nocturnal hours when they were most active. Therefore, road density could affect cougar harvest rates because cougar attraction to roads would increase the likelihood that tracks would be detected by a hunter. Where prey are concentrated during specific

seasons, managers should also consider separate seasonal cougar density estimates and distributions (Pierce et al. 1999), particularly since most hunting occurs in winter.

Manipulating cougar habitat would require alteration of large areas. The coniferous and deciduous woodland belts probably represent the most important habitat for cougars in central and northern Utah. Because cougars are restricted to these communities in winter, their availability and quality may be limiting factors. These areas also provide year-round habitat for some individuals. For these reasons, management efforts may be most effective if focused on cougar winter range. The montane woodlands are also susceptible to loss due to housing development and degradation due to alteration of the fire cycle. Conservation efforts focused on the montane woodlands would benefit cougars as well as mule deer, which are threatened by the continued loss of critical winter range. Efforts to improve mule deer range will improve its utility to cougars both by increasing deer numbers and enhancing hunting conditions. Increasing species diversity, understory layer, downfall or woody debris, mosaic conditions, and presence of rocky outcrops or boulder clusters would enhance habitat for cougars. It is unlikely that landforms could be manipulated across large extents, but if reclaiming mined or other previously disturbed areas, creating diverse topography would benefit cougars.

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APPENDICES

APPENDIX A. LAND COVER RECLASSIFICATION TABLES

Table A.1. Aggregation of ecological systems from Southwest Regional Gap Analysis Project land cover map (USGS 2004) within the study site boundary on the Oquirrh Mountains, Utah.

Type	New Class	Area (km^2)	% of Total Study Area	SWReGAP Code	SWReGAP Description	Area (km^2)	% of Total Study Area
1	CLIFF, CANYON, ROCKY SYSTEMS	24	2.80%	S050	Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland	16.9	2.80%
				S009	Inter-Mountain Basins Cliff and	1.8	0.30%
2	CONIFEROUS FOREST	39.2	4.60%	S034	Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodland	13.3	2.20%
				S032	Rocky Mountain Montane Dry-Mesic Mixed Coniferous Forest and	10.2	1.70%
				S030	Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	3	0.50%
				S028	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	1.3	0.20%
3	DECIDUOUS FOREST	37.3	4.40%	S023	Rocky Mountain Aspen Forest and Woodland	28.3	4.70%
4	DECIDUOUS WOODLAND	166.4	19.60%	S046	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	122.7	20.20%
				S024	Rocky Mountain Bigtooth Maple Ravine Woodland	28.6	4.70%
5	CONIFEROUS	107.5	12.70%	S040	Great Basin Pinyon-Juniper Woodland	93.7	15.40%
6	MONTANE SHRUBLAND	39.4	4.60%	S071	Inter-Mountain Basins Montane Sagebrush Steppe	39.1	6.40%
7	BASIN SHRUBLAND	105.8	12.50%	S015	Inter-Mountain Basins Playa	< 0.1	0.00%
				S054	Inter-Mountain Basins Big Sagebrush Shrubland	61.6	10.20%
				S055	Great Basin Xeric Mixed Sagebrush Shrubland	3.2	0.50%
				S065	Inter-Mountain Basins Mixed Salt Desert Scrub	0.4	0.10%

Table A.1. (continued). Aggregation of ecological systems from Southwest Regional Gap Analysis Project land cover map (USGS 2004) within the study site boundary on the Oquirrh Mountains, Utah.

Type	New Class	Area (km^2)	% of Total Study Area	SWReGAP Code	SWReGAP Description	Area (km^2)	% of Total Study Area
				S079	Inter-Mountain Basins Semi-Desert Shrub Steppe	2.8	0.50%
				S096	Inter-Mountain Basins Greasewood Flat	1.8	0.30%
8	GRASSLAND	27.7	3.30%	S085	Southern Rocky Mountain Montane-Subalpine Grassland	10.3	1.70%
				S090	Inter-Mountain Basins Semi-Desert Grassland	8.7	1.40%
				D06	Invasive Perennial Grassland	2.8	0.50%
9	RIPARIAN	17.7	2.10%	S118	Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland	9.3	1.50%
				S100	North American Arid West Emergent Marsh	0.2	0.00%
10	AGRICULTURE	116.5	13.70%	N80	Agriculture	47.1	7.80%
11	DISTURBED/BARREN	61	7.20%	D03	Recently Mined or Quarried	39.1	6.50%
				D08	Invasive Annual Grassland	10.3	1.70%
				D09	Invasive Annual and Biennial Forbland	0.5	0.10%
12	DEVELOPED	104.2	12.30%	N21	Developed, Open Space - Low intensity	33.7	5.60%
				N22	Developed, Medium - High Intensity	15.9	2.60%
	OPEN WATER*			N11	Open Water	2.7	0.30%

* Excluded from analysis.

Table A.2. Aggregation of ecological systems from Southwest Regional Gap Analysis Project land cover map (USGS 2004) on within the study site boundary on Monroe Mountain, Utah.

Type	New Class	Area (km^2)	% of Total Study Area	SWReGAP Code	SWReGAP Description	Area (km^2)	% of Total Study Area
1	CLIFF, CANYON, ROCKY SYSTEMS	36.1	1.90%	S002	Rocky Mountain Alpine Bedrock and Scree	0.3	<0.1%
				S006	Rocky Mountain Cliff and Canyon	26.7	1.40%
				S010	Colorado Plateau Mixed Bedrock Canyon and Tableland	3.1	0.20%
				S050	Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland	6	0.30%
2	CONIFEROUS FOREST	141.7	7.40%	S028	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	81.7	4.20%
				S030	Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	32.3	1.70%
				S032	Rocky Mountain Montane Dry-Mesic Mixed Conifer Forest and Woodland	13	0.70%
				S034	Rocky Mountain Mesic Mixed Conifer Forest and Woodland	14.7	0.80%
3	DECIDUOUS FOREST	162.7	8.40%	S023	Rocky Mountain Aspen Forest and Woodland	115.3	6.00%
				S042	Inter-Mountain West Aspen-Mixed Conifer Forest and Woodland Complex	47.4	2.50%
4	DECIDUOUS WOODLAND	72.7	3.80%	S046	Rocky Mountain Gambel Oak-Mixed Montane Shrubland	72.7	3.80%
5	CONIFEROUS WOODLAND	586.6	30.50%	S036	Rocky Mountain Ponderosa Pine Woodland	11.9	0.60%
				S039	Colorado Plateau Pinyon-Juniper Woodland	573.9	29.80%
				S040	Great Basin Pinyon-Juniper Woodland	0.8	<0.1%

Table A.2 (continued). Aggregation of ecological systems from Southwest Regional Gap Analysis Project land cover map (USGS 2004) on within the study site boundary on Monroe Mountain, Utah.

Type	New Class	Area (km^2)	% of Total Study Area	SWReGAP Code	SWReGAP Description	Area (km^2)	% of Total Study Area
6	MONTANE SHRUBLAND	300	15.60%	S071	Inter-Mountain Basins Montane Sagebrush Steppe	300	15.60%
7	BASIN SHRUBLAND	467.9	24.30%	S054	Inter-Mountain Basins Big Sagebrush Shrubland	439.7	22.80%
				S050	Colorado Plateau Mixed Low Sagebrush Shrubland	6.6	0.30%
				S065	Inter-Mountain Basins Mixed Salt Desert Scrub	7.6	0.40%
				S079	Inter-Mountain Basins Semi-Desert Shrub Steppe	12.2	0.60%
				S096	Inter-Mountain Basins Greasewood Flat	1.8	0.10%
8	GRASSLAND	16.8	0.90%	S081	Rocky Mountain Dry Tundra	1.4	0.10%
				S083	Rocky Mountain Subalpine Mesic Meadow	0.3	<0.1%
				S085	Southern Rocky Mountain Montane-Subalpine Grassland	10.4	0.50%
				S102	Rocky Mountain Alpine-Montane Wet Meadow	4.7	0.30%
9	RIPARIAN	12	0.60%	S091	Rocky Mountain Subalpine-Montane Riparian Shrubland	0.3	<0.1%
				S093	Rocky Mountain Lower Montane Riparian Woodland and Shrubland	11.7	0.60%
10	AGRICULTURE	89.1	4.60%	N80	Agriculture	89.1	4.60%
11	DISTURBED/BARREN	14.5	0.80%	S011	Inter-Mountain Basins Shale Badland	1.8	0.10%
				D02	Recently Burned	2.7	0.10%
				D08	Invasive Annual Grassland	0.5	<0.1%
				D11	Recently Chained Pinyon-Juniper	9.5	0.50%

Table A.2 (continued). Aggregation of ecological systems from Southwest Regional Gap Analysis Project land cover map (USGS 2004) on within the study site boundary on Monroe Mountain, Utah.

Type	New Class	Area (km^2)	% of Total Study Area	SWReGAP Code	SWReGAP Description	Area (km^2)	% of Total Study Area
12	DEVELOPED	9.1	0.50%	N21	Developed, Open Space – Low Intensity	6.8	0.40%
				N22	Developed, Medium-High Intensity	2.3	0.10%
	OPEN WATER*			N11	Open Water	16.3	0.80%

APPENDIX B. MAPS OF RECLASSIFIED LAND COVER TYPES

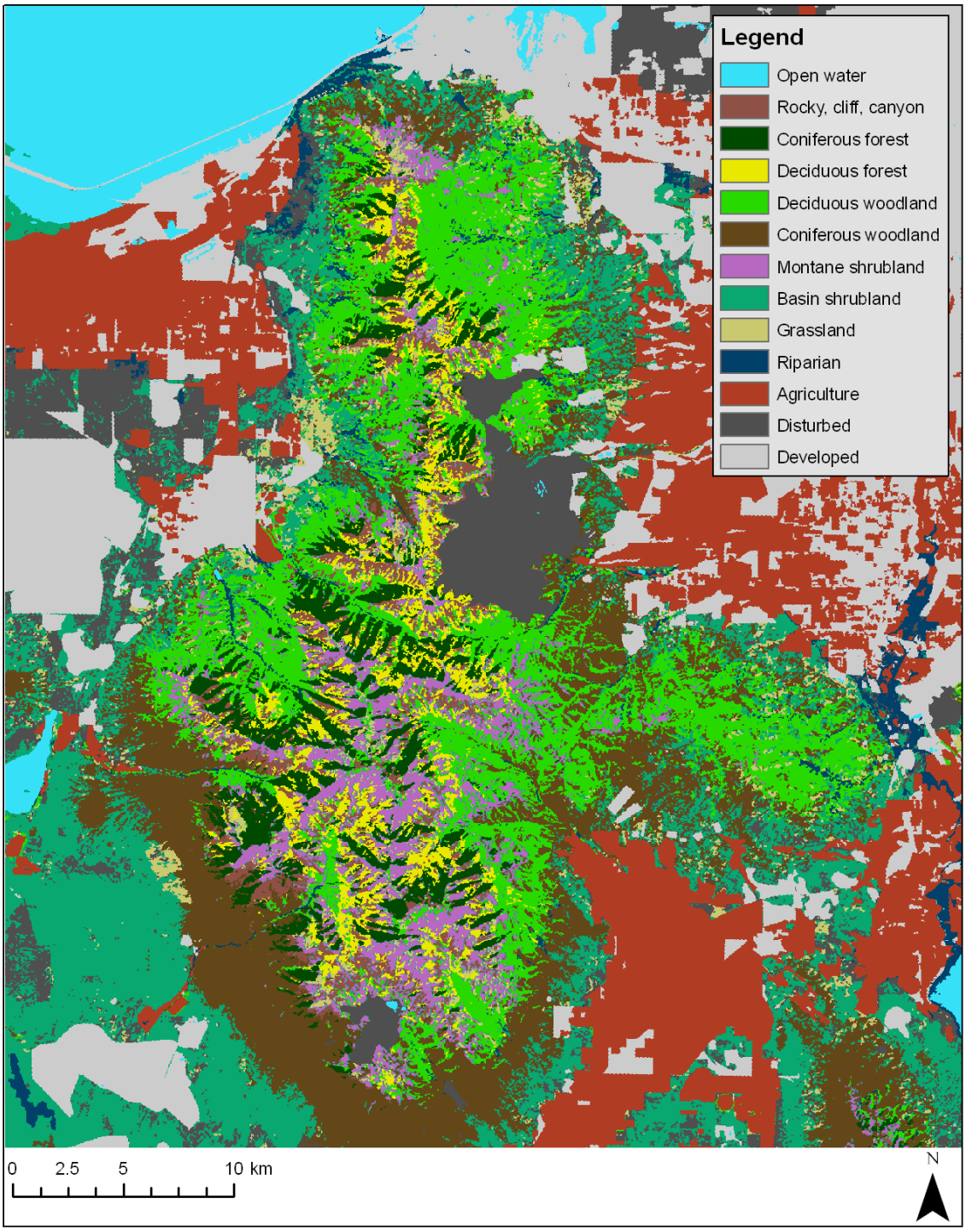

Figure B.1. Land cover types on the Oquirrh Mountains, Utah, reclassified from Southwest Regional GAP map (USGS 2004).

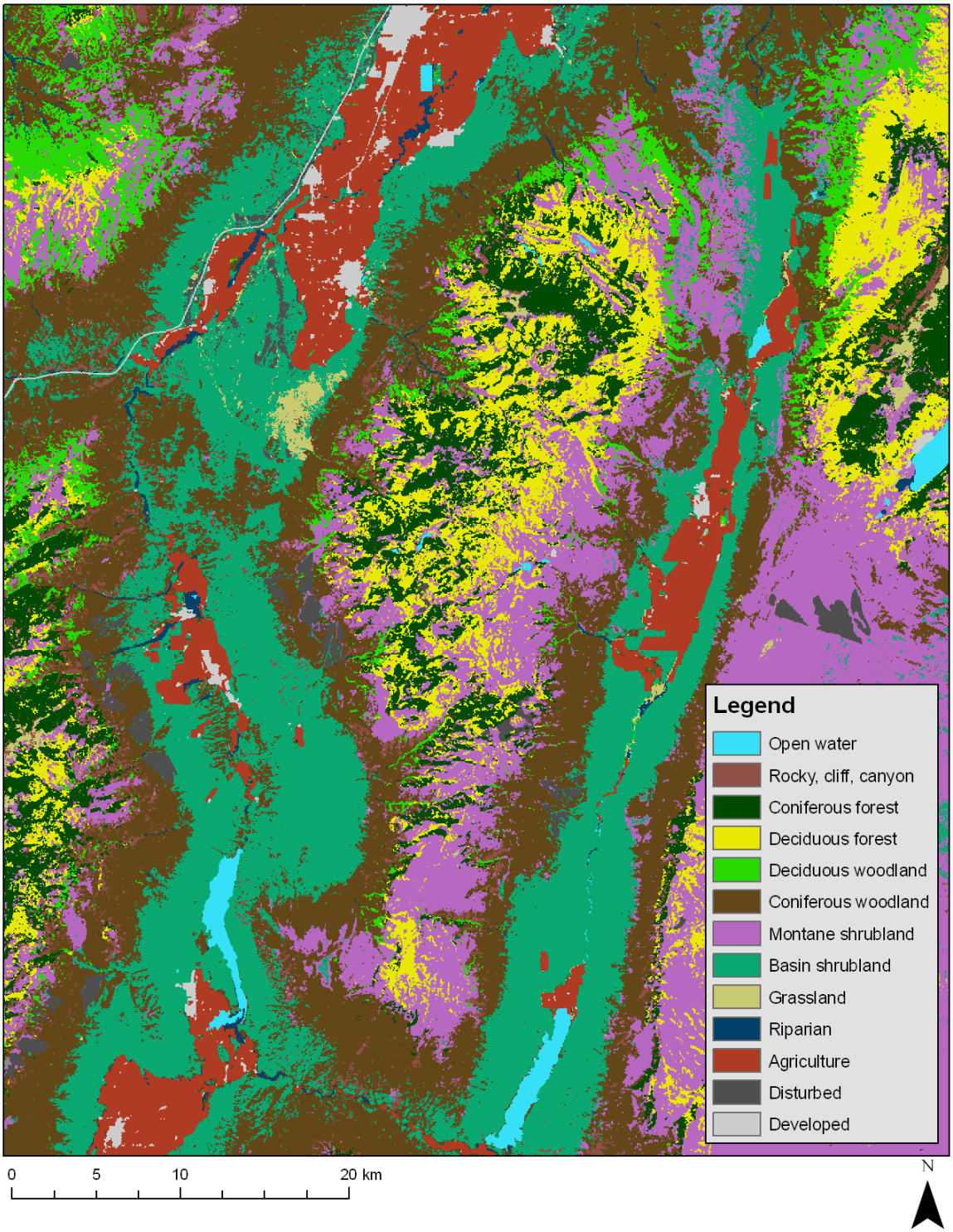

Figure B.2. Land cover types on Monroe Mountain, Utah, reclassified from Southwest Regional GAP map (USGS 2004).

APPENDIX C. LAND FORM RECLASSIFICATION TABLE

Table C.1. Five-class aggregation of a 10-class landform model, which was generated using thresholds for slope and for 2 topographic position indices (TPI) (Jenness (2005).

5-class landform description	10-class landform description	Small neighborhood (500 m) TPI criteria	Large neighborhood (2000 m) TPI criteria	Slope criteria
CANYONS & DRAINAGES	Canyons, deeply incised streams	TPI ≤ -1	TPI ≤ -1	n/a
	Midslope drainages, shallow valleys	TPI ≤ -1	-1 < TPI < 1	n/a
	Upland drainages, headwaters	TPI ≤ -1	TPI ≥ 1	n/a
STEEP SLOPES	U-shaped valleys	-1 < TPI < 1	TPI ≤ -1	n/a
	Upper slopes	-1 < TPI < 1	TPI ≥ 1	n/a
	Local ridges/hills in valleys	TPI ≥ 1	TPI ≤ -1	n/a
VALLEY BOTTOMS & MESAS	Plains small	-1 < TPI < 1	-1 < TPI < 1	≤ 5°
GENTLE SLOPES	Open slopes	-1 < TPI < 1	-1 < TPI < 1	> 5°
RIDGES & HILL TOPS	Midslope ridges, small hills in plains	TPI ≥ 1	-1 < TPI < 1	n/a
	Mountain tops, high ridges	TPI ≥ 1	TPI ≥ 1	n/a

APPENDIX D. COUGAR HOME RANGES AT THE OQUIRRH MOUNTAINS STUDY SITE IN VARIOUS YEARS

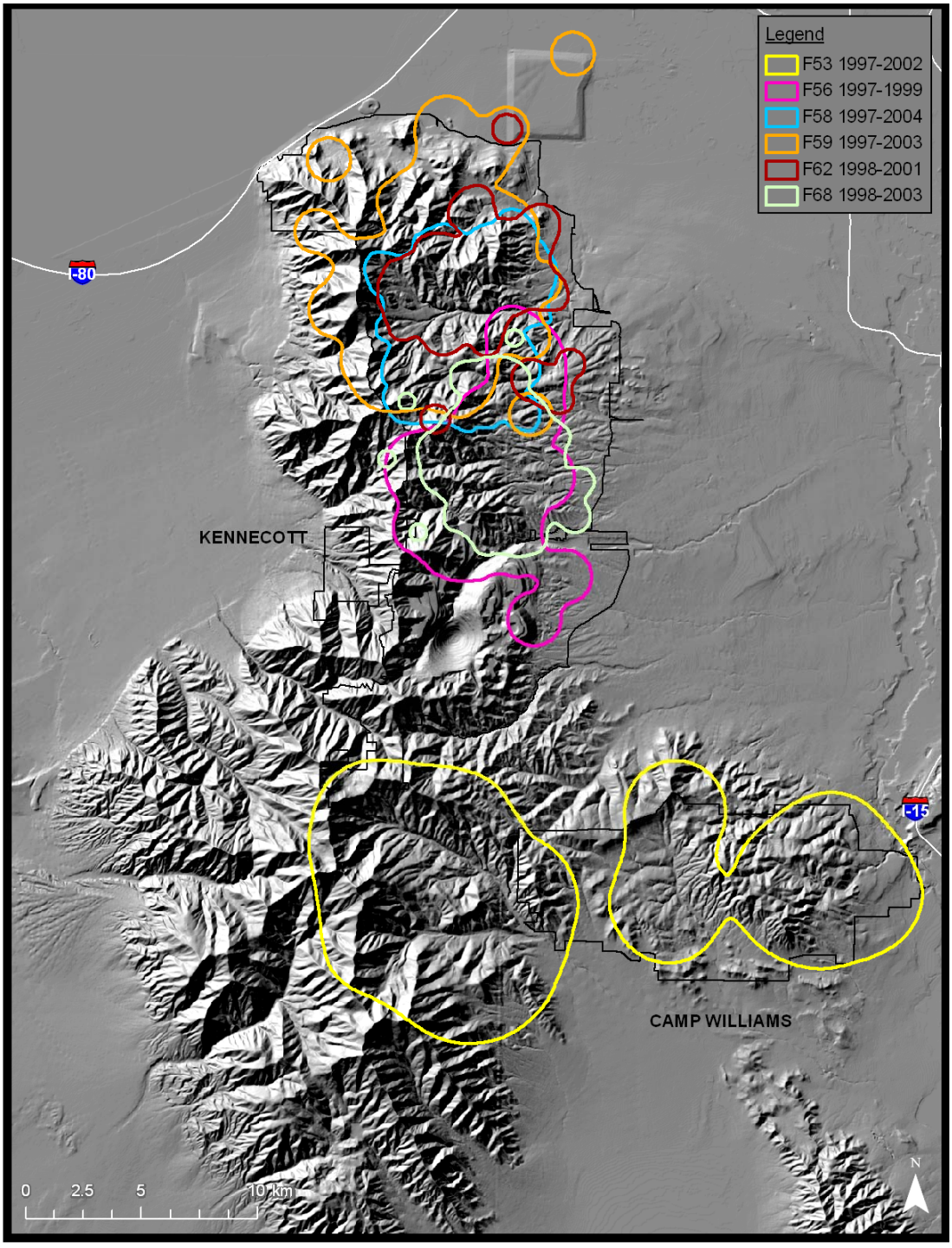

Figure D.1. Multi-year 95% fixed kernel home ranges for female cougars monitored on the Oquirrh Mountains, Utah in the year 1999, estimated from diurnal aerial and GPS collar telemetry data.

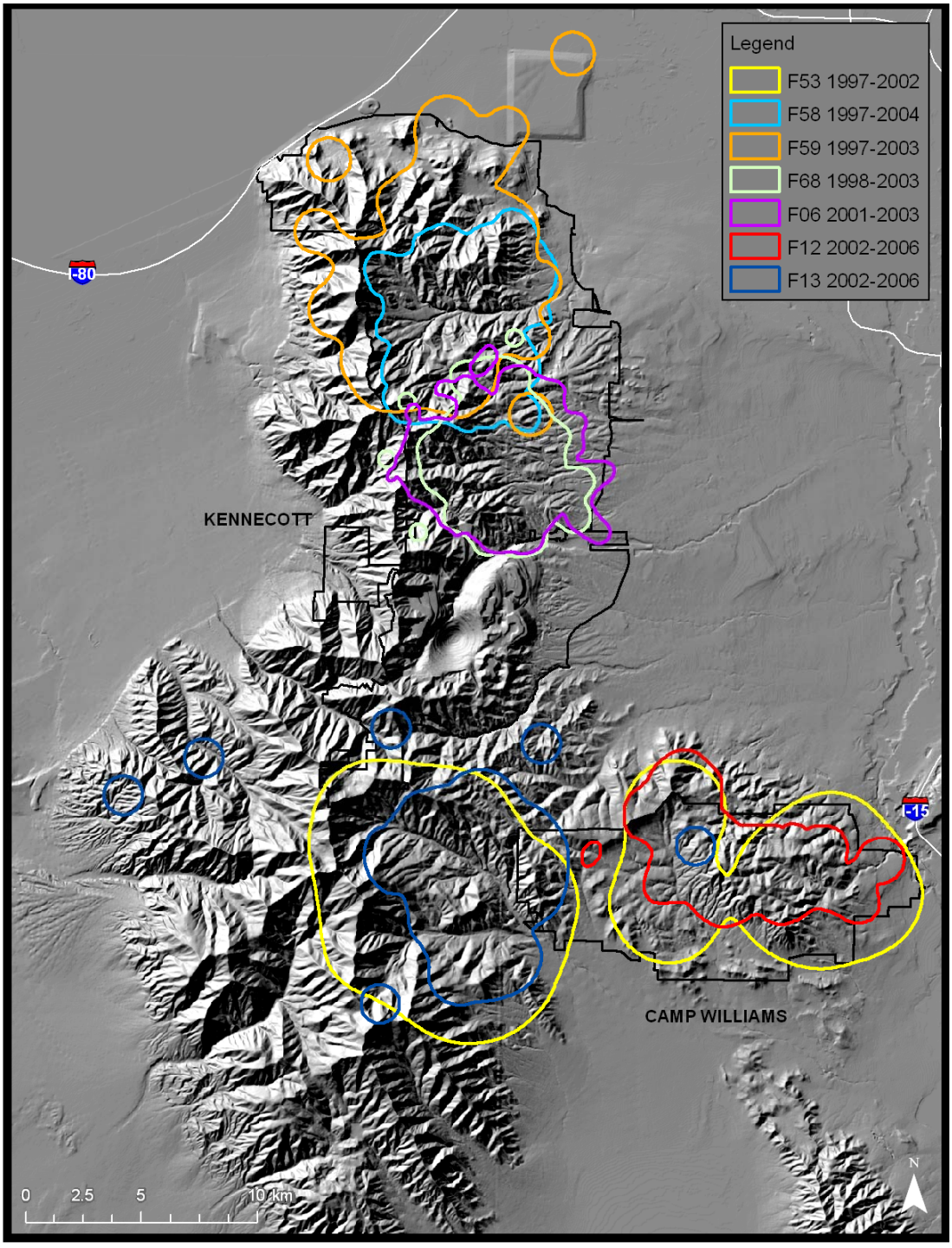

Figure D.2. Multi-year 95% fixed kernel home ranges for female cougars monitored on the Oquirrh Mountains, Utah in the year 2002, estimated from diurnal aerial and GPS collar telemetry data.

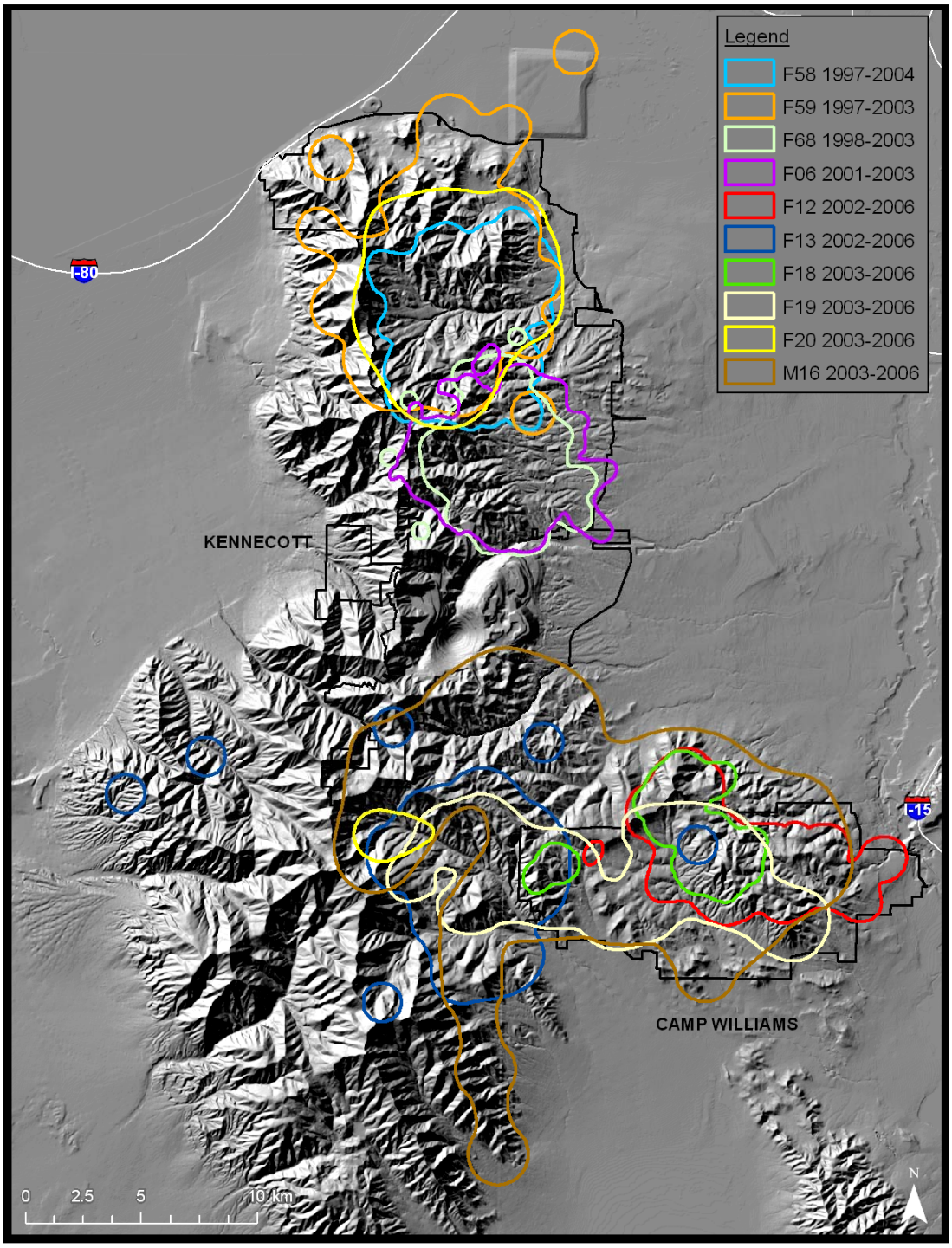

Figure D.3. Multi-year 95% fixed kernel home ranges for female and male cougars monitored on the Oquirrh Mountains, Utah in the year 2003, estimated from diurnal aerial and GPS collar telemetry data.

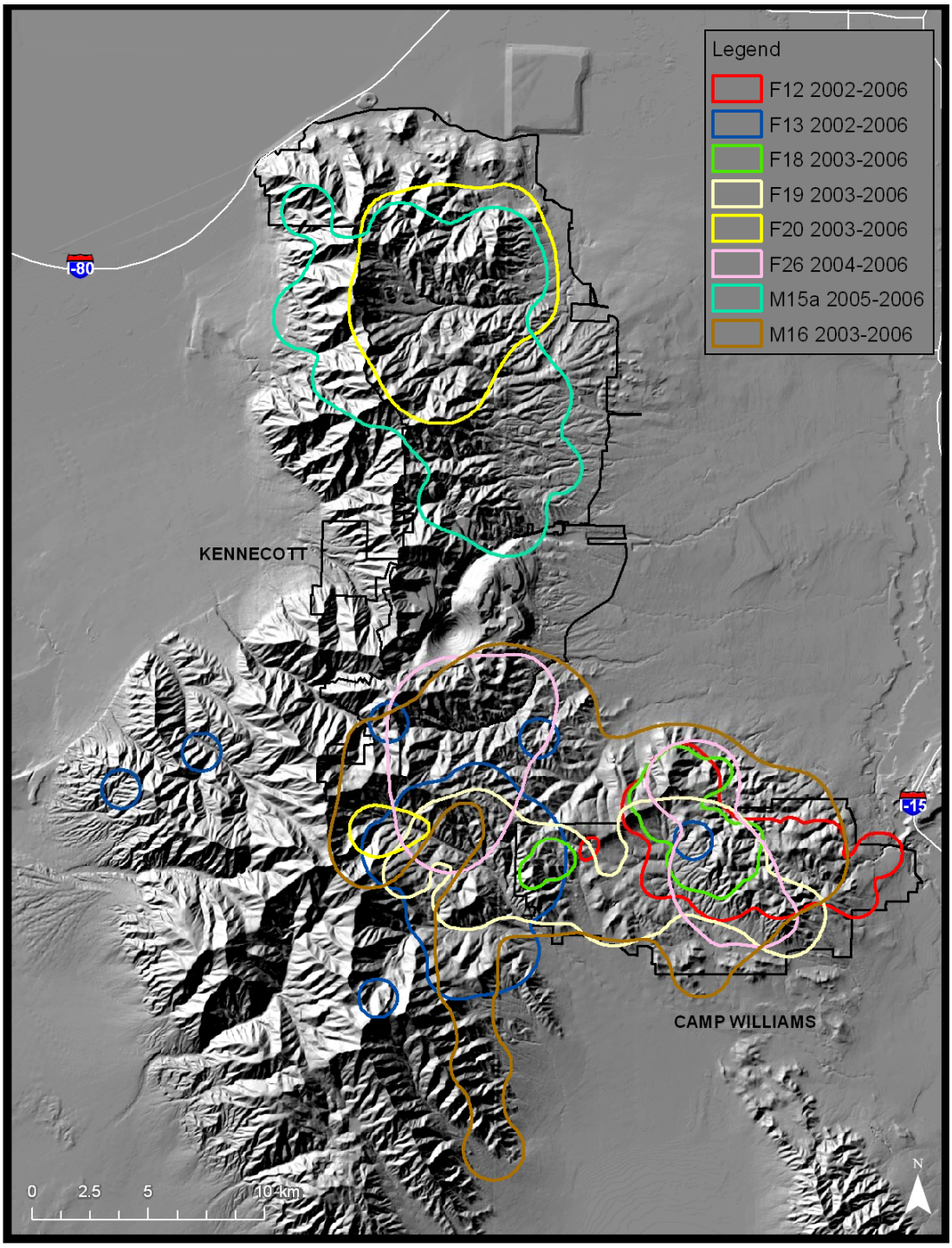

Figure D.4. Multi-year 95% fixed kernel home ranges for female and male cougars monitored on the Oquirrh Mountains, Utah in the year 2005, estimated from diurnal aerial and GPS collar telemetry data.

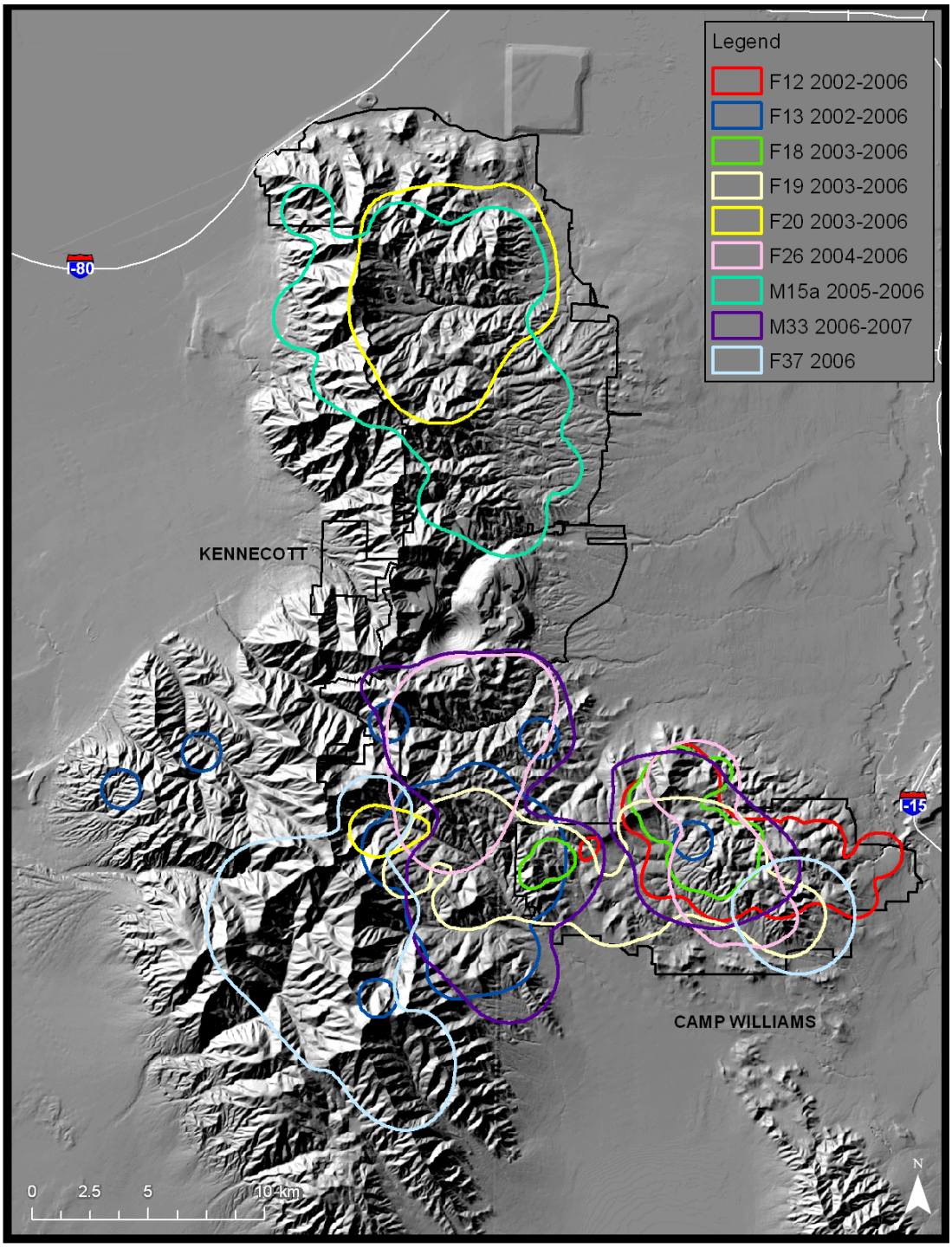

Figure D.5. Multi-year 95% fixed kernel home ranges for female and male cougars monitored on the Oquirrh Mountains, Utah in the year 2006, estimated from diurnal aerial and GPS collar telemetry data.

APPENDIX E. COUGAR HOME RANGES AT THE MONROE MOUNTAIN STUDY SITE IN VARIOUS YEARS

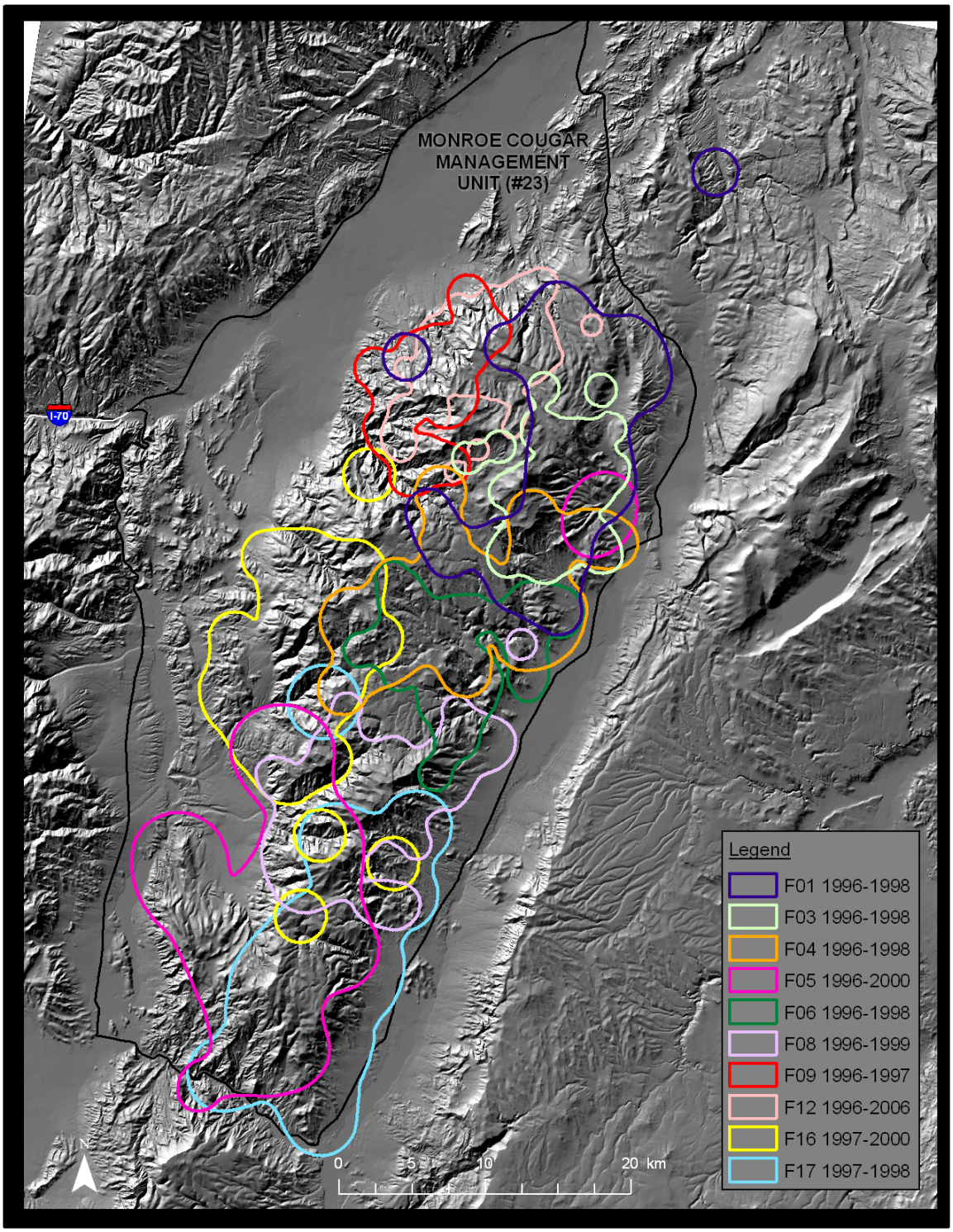

Figure E.1. Multi-year 95% fixed kernel home ranges for female cougars monitored on Monroe Mountain, Utah in the year 1997, estimated from diurnal aerial telemetry data.

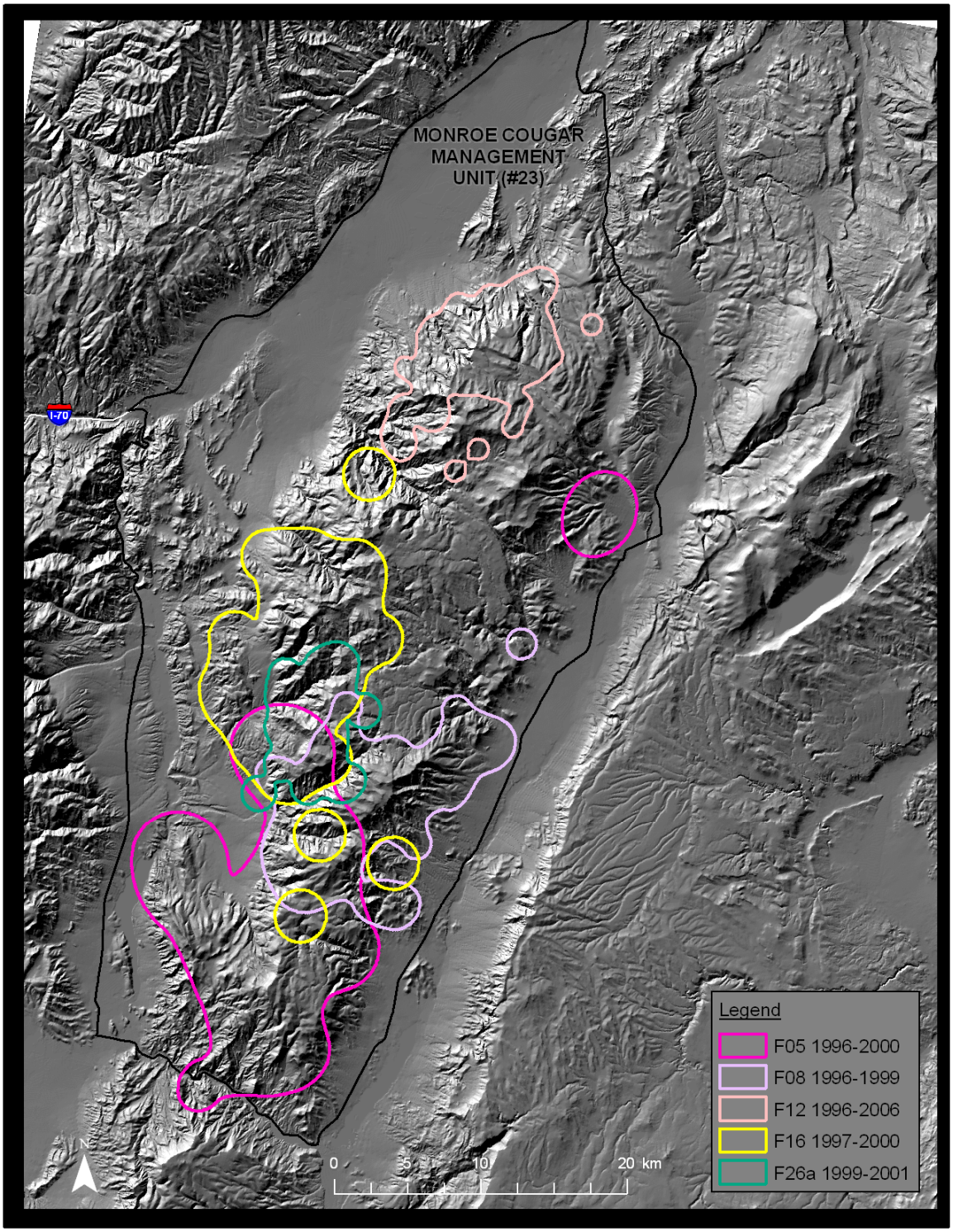

Figure E.2. Multi-year 95% fixed kernel home ranges for female cougars monitored on Monroe Mountain, Utah in the year 1999, estimated from diurnal aerial telemetry data.

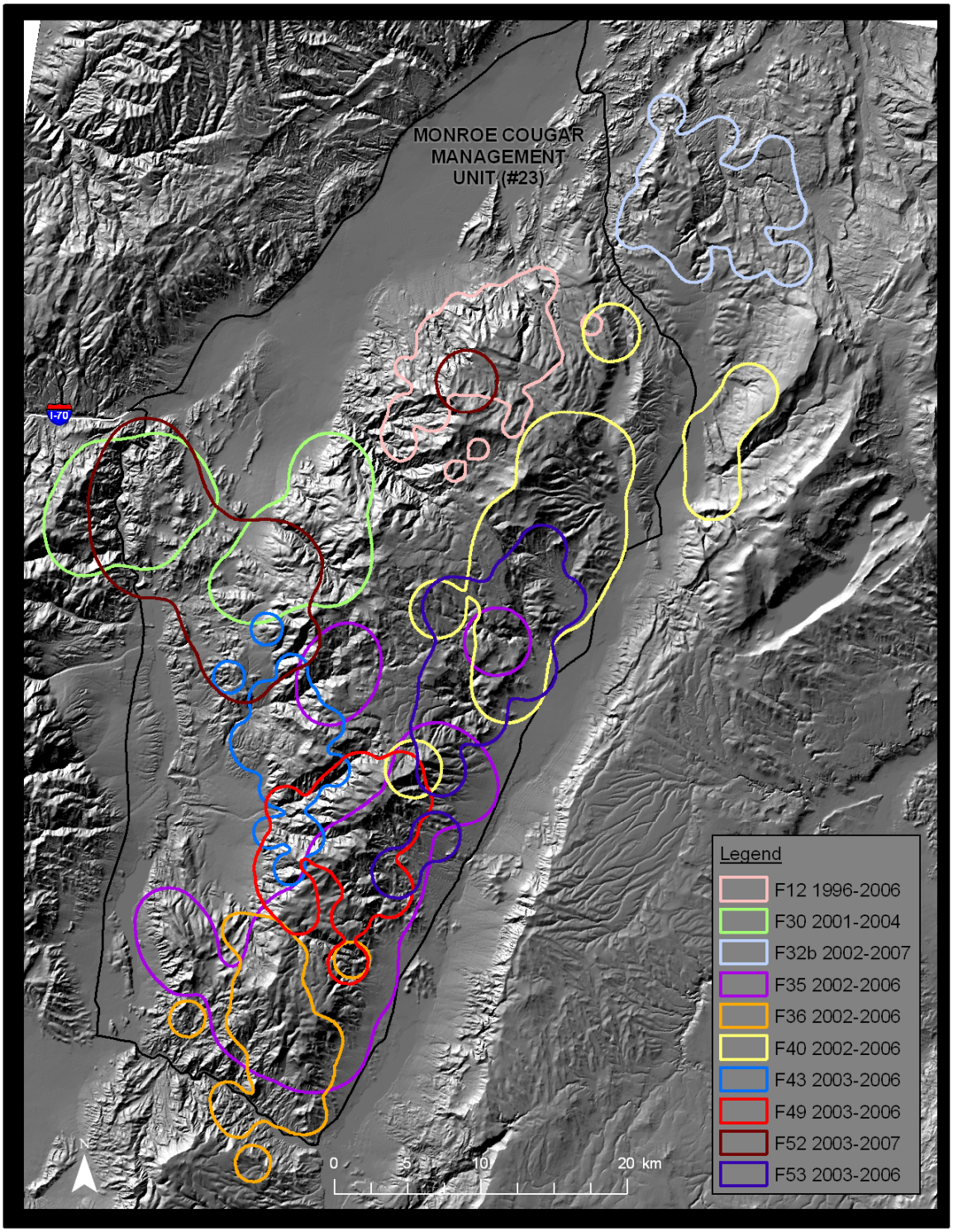

Figure E.3. Multi-year 95% fixed kernel home ranges for female cougars monitored on Monroe Mountain, Utah in the year 2003, estimated from diurnal aerial telemetry data.